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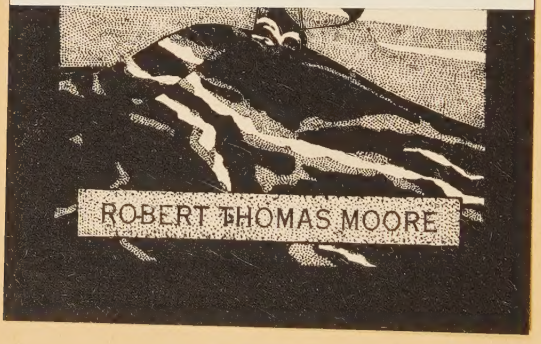

To
Dad
From Paul.

Christmas 1929.

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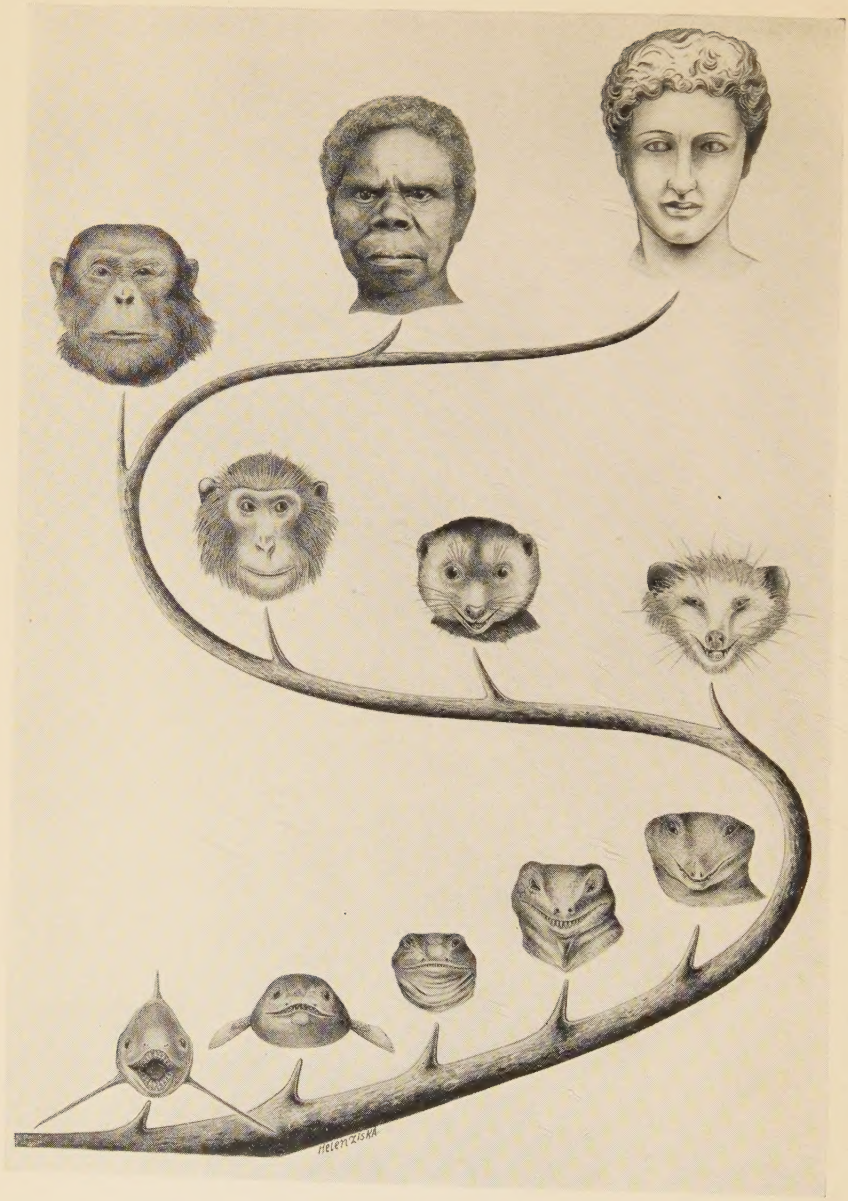

OUR FACE FROM FISH TO MAN.

1. Devonian shark; 2. Upper Devonian air-breathing, lobe-finned fish; 3. Lower Carboniferous amphibian; 4. Permo-Carboniferous reptile; 5. Triassic mammal-like reptile; 6. Cretaceous mammal; 7. Lemuroid primate; 8. Recent Old World monkey; 9. Chimpanzee; 10. Tasmanian; 11. Roman athlete.

For details see p. xiii.

OUR FACE FROM FISH TO MAN

A Portrait Gallery of Our Ancient Ancestors and Kinsfolk together with a Concise History of Our Best Features

BY

WILLIAM K. GREGORY

Professor of Vertebrate Palæontology, Columbia University; Associate in Anthropology and Curator of the Departments of Ichthyology and Comparative Anatomy, American Museum of Natural History; Member of the National Academy of Sciences, etc.

WITH A FOREWORD BY

WILLIAM BEEBE

With 119 Illustrations

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OUR FACE FROM FISH TO MAN

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TO

HENRY FAIRFIELD OSBORN

FOREWORD

BY WILLIAM BEEBE

A FOREWORD to a volume such as the present one of Dr. Gregory's is as superfluous as would be the retention of the third eye, the Cyclopean one, of our ancestors, in the center of our forehead today. No more wonderful subject for a volume could be imagined than the evolution of the human face, and no more competent author than William K. Gregory. The result seems to me eminently satisfactory.

If the reader's interest is real but cursory, let him do nothing but look at the illustrations. They will ensure a thousand percent interest to every walk along Fifth Avenue or Regent Street. If pressure of other interests permits only an hour's perusal, or complete lack of natural history knowledge requires facts to be strained through the mesh of popular language, read but the preface and the first few paragraphs of each chapter. Taken as a whole this is not a "popular" book in

the sense of a superficial one. The details of evolution of our eyes, ears, nostrils, mouth—these are too delicate, too intricate for words of one syllable. Yet to read and understand this volume requires no more concentrated attention than the remembrance of the highest diamond in the ninth trick, or to what Steel Preferred fell in the Autumn of 1914.

I advise no Fundamentalist or Anti-Evolutionist to read it, for if he have no sense of humor he will not understand it, and if he have, his belief will be like Dunsany's King who "was as though he never had been." If with Bergson we believe that the origin of laughter was cruelty, then an S. P. C. to something should be formed to prevent the spectacle of a Fundamentalist's face functioning with the third eyelid of a bird, the ear-point of a deer, the honorable scars of most ancient gills, and with his lip-lifting muscles in full action as he sneers at truth. A moment's thought of these few characters presents a new viewpoint on what we are wont to call the "lower" animals, for if our third eyelid were more than a degenerate flap we, like an eagle, could look straight at the sun; if our ears could straighten and turn as once, the lives of

pedestrians would be safer; if the ghosts of gills were still functional, drowning would be impossible, and if the fang-revealing sneer showed less degenerate canines, we might have a more physically wholesome fear of cavilers against the doctrine of Evolution.

The impregnable array of facts gleaned through the centuries of man's intellectual supremacy proves beyond all question the gradual rise toward human perfection of the various components of the face, and this confirms our precious organs of sense as most noble gateways of the human mind and soul. Kindness, gentleness, tactfulness, patience, can flow out through only these channels. It is a worthy thing to have written a book about them; it is a fortunate chance to be able to read it.

PREFACE

ACCORDING to popular standards of civilized peoples, men of one's own race and tongue were called "men," "warriors," "heroes," but people of other races were "barbarians," "unholy ones," "foreign devils." The founder of one's own clan was often considered to be the son of a deity, while the barbarians were the descendants of monkeys or other wild animals. Or the first man was created perfect, in the image of God. One's own family, of course, was fairly true to type but sin had played havoc with the features of other races. To believe all this was comforting to one's own "face" in a world where the inferiority complex occasionally haunted even kings.

Imagine then the effect of telling one-hundred-percent Americans that they are not the descendants of the god-like Adam but are sons and daughters of *Dryopithecus*, or of some nearly allied genus of anthropoid apes that lived in the Miocene

age,—and that before that they had long tails and ate grubs and beetles!

If the reader is curious to know the worst he will find it in these pages. There even his own great-grandfather—a Jove-like patriarch with ample beard, piercing eyes and an aquiline nose—will be subjected to unsparing analysis. It will be shown how much the proud old gentleman was indebted to a long line of freebooting forbears that struggled for a precarious living in the sea, on muddy flats, on the uplands or in the trees—æons before Adam delved or Eve span. In detail it will even be charged that the real founder of the family was not the powerful settler to whom the king gave a grant of land extending far back from the river, but a poor mud-sucking protochordate of pre-Silurian times; that when in some far-off dismal swamp a putrid prize was snatched by scaly forms, their facial masks already bore *our* eyes and nose and mouth.

Accordingly this little book can hardly expect much popularity either in Tennessee, where the very idea of evolution is anathema, or in the metropolitan strongholds where pithecophobia is still prevalent and man's complete superiority to the

all too man-like apes is somewhat nervously stressed.

Nor can the author hope for much favor from the public, that wants only results and is willing to spend a billion dollars annually on cosmetics and safety razors. For this book does not pretend to tell how to improve one's face but only how and why one has one.

At best then it can only hold a magic mirror up to proud man and bid him contemplate his own image—a composite of an infinitely receding series of faces,—human, prehuman, anthropoid, long-snouted, lizard-like,—stretching back into the shadows of endless time.

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C. *Megalichthys*, inner side. (After Watson.)

D. *Trimerorhachis*, inner side. (After Williston.)

E. Recent turtle embryo, inner side. (After Parker.)

Abbreviations of names of bones: *ang*, angular; *art*, articular; *cor*, coronoids (I, II); *dn*, dentary; *preart*, prearticular; *pospl*, postsplenial; *spl*, splenial; *surang*, surangular bone.

In the embryo turtle Meckel's cartilage is very plainly seen on the inner side of the jaw, extending the full length of the jaw. The rear end forms the articular bone of the adult.

These jaws are made mostly of the dermal sheathing bones that in the embryo surround the primary carti-

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in the inner lining of the nerve tube or brain, with the "rods" turned away from the light.

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The broken line indicates the position of the pouch from the tubo-tympanal cavity as inferred by Watson and Sushkin.

B. Rear view of the skull of *Permocynodon*, showing the perforate stapes in position. (After Sushkin.)

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OUR FACE FROM FISH TO MAN

OUR FACE FROM FISH TO MAN

PART I

PORTRAIT GALLERY OF OUR ANCIENT RELATIVES AND ANCESTORS

THE VALUE OF A FACE

For a billion years or more the ceaseless game of life has been concerned with the capture and utilization of energy for the benefit of the individual and with the rhythmic storage and release of energy for the reproduction of the race.

In all ages and in all branches of the animal kingdom a face of some sort has been indispensable to all but sessile animals, just because a face is concerned primarily with:

The detection of desirable sources of energy;

The direction of the locomotor machinery toward its goal;

The capture and preliminary preparation of the energy-giving food.

Among the highest animals the face acts also as a lure for the capture of a mate.

In nearly all the lower vertebrate animals, however, the most constant and dominating element of the face is the gateway formed by the mouth and arching jaws to the "primitive gut" or digestive tract.

Around this architectural centerpiece the higher facial designs gradually developed.

THE BEGINNINGS OF OUR FACE

Doubtless it is a far cry from the lowly Slipper Animalcule, whose face consists only of a gash in the side of its moccasin-like body, to the human face divine, but among the thousands of known living and fossil forms Nature has left us a number of significant vestiges on the long pathway of creation. Among the more primitive of the many-celled animals the jellyfishes consist essentially of a two-layered parachute-like sac, the inner layer serving as a primitive gut, the outer layer chiefly as an envelope. The mouth of the sac is greatly puckered and the folds are produced into tentacles, often endowed with nettle-like, stinging threads. A diffuse nerve net extends everywhere

between the inner and the outer layer and is concentrated into a ring around the mouth. This mouth is far from being homologous with our own. It represents at most the "primitive streak" of the early embryos of vertebrate animals. Never-

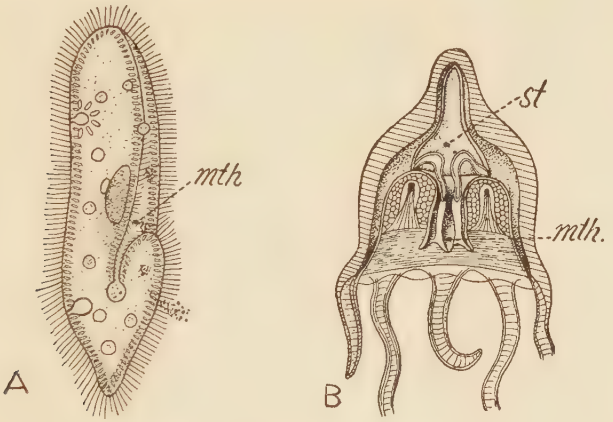

Fig. 1. The First Mouths.

Slipper animalcule (A) with gash-like mouth; Jellyfish (B), a two-layered sac with primitive mouth. (Both after Parker and Haswell.)
For details, see p. xiii.

theless it was the starting-point for further developments.

The direct line of ascent toward the vertebrates is not yet definitely known and we can only surmise what the next few steps may have been. The flatworms appear to represent highly developed descendants of the jellyfish group, which had abandoned the drifting habits of their remote

ancestors and taken to living on the bottom in shallow water. The simple pulsations of a bell-shaped body, which were sufficient for jellyfishes, were modified into writhings or contractions in definite directions. Anyhow, radial symmetry gave way to bilateral symmetry, the animals began to progress in a fore-and-aft direction and the sharp differentiation of heads and tails was in full play.

The early evolution of a primitive head is also well illustrated in certain flatworms (Fig. 2A), in which the slender nerve threads are drawn together to form the first rudiments of a brain and a very simple type of eyes is attained. In the annelid worms the head is further advanced, since the mouth is now surrounded by various accessory organs for the testing of the food, by horny jaws moved by muscles for the capture of the food, by elaborate eyes and by an extensive fusion of nerve fibers into an incipient brain. The trilobites and higher crustaceans (Fig. 2B) carry the story onward, showing us how some of the jointed projections from the sides of the body, which had originally been developed as primitive legs, very early began to serve the mouth by drawing, kick-

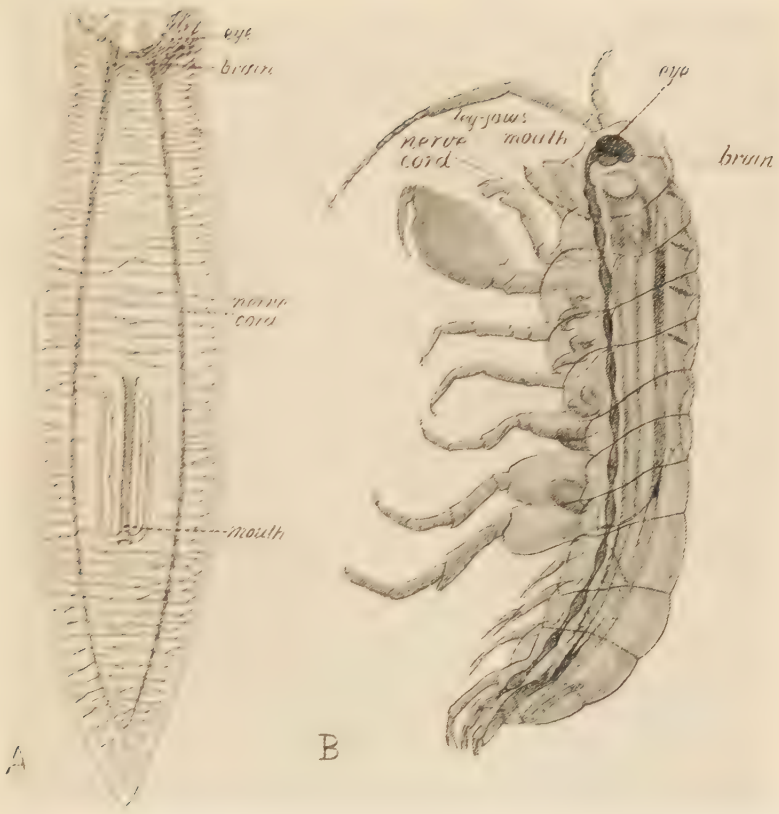

FIG. 2. TWO EARLY STAGES IN THE EVOLUTION OF A HEAD (AFTER PARKER AND HASWELL).

Flatworm (A), showing a head-and-tail differentiation, including the beginnings of a brain and of eyes; Sand-flea (B), showing the interrelations of eye, brain, mouth, leg-jaws and nerve cord.

For details see p. xiii.

ing or pushing the food within its reach, these mouth-legs finally culminating in the various and highly refined burglar tools so well wielded by the swarming hosts of insects.

According to Professor Patten of Dartmouth, the vertebrates were derived from the arachnid stem—an ancient branch of the jointed animals (arthropods), that is represented today by *Limulus*, the "king-crab" (which is not a crab at all), and by the arachnids (scorpions and spiders). But if these disagreeable creatures are our remote relatives, then the highly developed head which they had acquired after so many millions of years of struggle all had to be largely made over when the vertebrate stage of organization was reached. They had to sacrifice their elaborate leg-jaw apparatus, their very mouths were stopped and a new mouth and jaws were formed, their eyes were turned upside down and inside out and a new set of swimming organs had to be developed.

According to the more orthodox view, the vertebrates from their earliest stages stood in wide contrast to the crustaceans, arachnids and insects. For while both groups comprise segmental animals,

moving in a fore-and-aft direction and building up a complex head through the fusion of simple segments, yet the arthropods developed their jaws out of jointed locomotor appendages while the vertebrates utilized for this purpose the cartilaginous bars of the first two gill pouches. According to Patten's view the fossil ostracoderms (Fig. 4) were more or less intermediate between these two great groups; but the objections to this view are formidable.

No matter from what group of invertebrates the vertebrates may have sprung, their origin took place many hundreds of millions of years after the first synthesis of living matter from less complex substances. When the first fishes took form the seas already swarmed with thousands of species of marine invertebrates,—protozoans, sponges, corals, trilobites, crustaceans, brachiopods, arthropods, molluscs, etc., and so far as the marine invertebrates were concerned, all the major problems of feeding, locomotion, sexual and asexual reproduction had been solved æons ago. And when the vertebrates started on their long career they too had already solved all the same fundamental problems by rigorously sacrificing much of their old

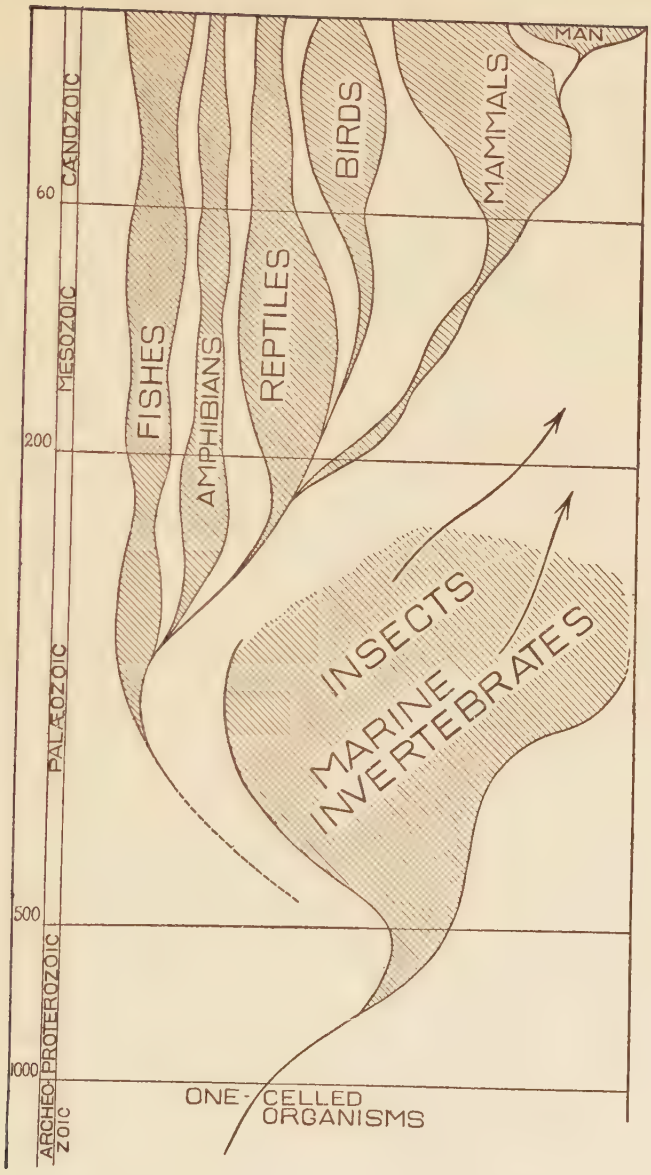

Fig. 3. The Rise of the Vertebrates in Geologic Times. Figures at left give estimated time in millions of years.

equipment and by profoundly changing what was left of their original heritage. The earliest known vertebrates (or more properly, chordates) are indubitably far nearer to us in geologic time and in the ground-plan of their whole organization than they were to the first living creatures; even their faces reveal them, as we shall presently see, as early kinsfolk of ours; the real beginnings of our facial type are either hidden in still unexplored rocks of pre-Silurian ages or wiped out forever by the destructive forces of erosion. From the viewpoint of earth history as a whole, even the earliest vertebrates of Silurian times (Fig. 4) rank among the younger children of life, yet from the viewpoint of mankind their antiquity is at first inconceivably vast, since according to all recent geological inquiry, it must be reckoned in hundreds of millions of years.

The recent monographic researches of Kiær and especially of Stensiö upon the amazingly well preserved ostracoderms of the Silurian and Devonian ages of Norway and of Spitzbergen have definitely shown that these curious forms are more or less directly ancestral to the hagfishes and lampreys of the present day, which comparative

anatomists have long regarded as standing far below the grade of the sharks in the scale of vertebrate life. In some of these fossils the infil-

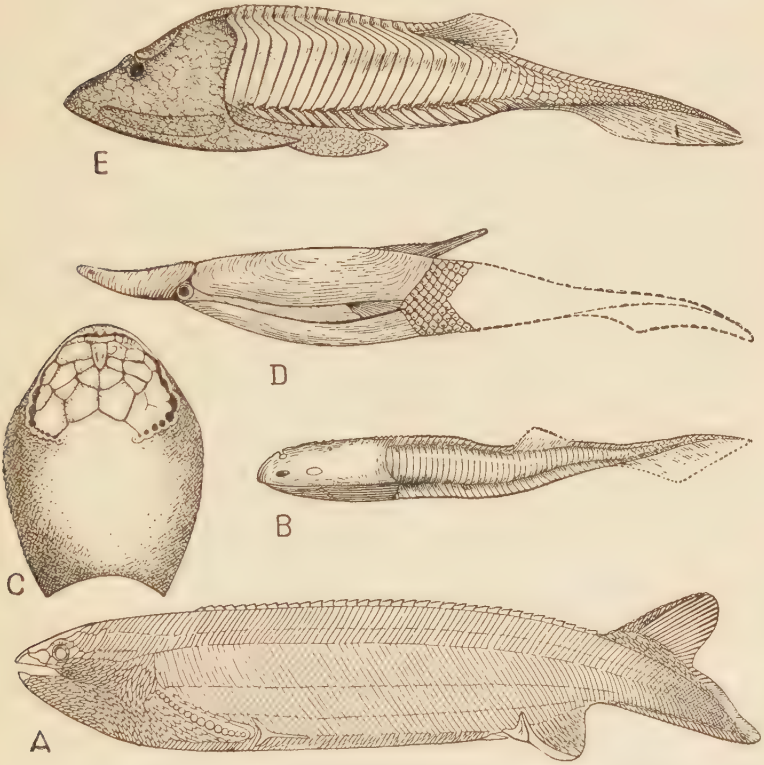

FIG. 4. SOME OF OUR EARLIEST KNOWN KINSFOLK. UPPER SILURIAN AND DEVONIAN OSTRACODERMS.

For details, see pp. xiii, xiv.

trated mud has made a natural cast of even the principal nerves and blood vessels of the head, so that Stensiö has been able to show that they com-

pare very closely in the ground-plan of the anatomy of their heads with the larval stages of the lampreys.

In all these lowly creatures as well as in ourselves the head is essentially the complex of sense organs, brain and brain covering, mouth and throat, by means of which the creature is directed to its food and enabled to engulf it.

THE SHARK'S FACE AND OURS

The ancestors of the higher vertebrates did not settle down and become specialized bottom-living fishes but long maintained themselves in the fierce competition of free-swimming, predaceous types. Whatever the first steps leading toward the vertebrate head may have been, the shark shows us our own facial anatomy stripped of all elaborations and reduced to simplest terms. Like Shylock, the shark might well plead that he has eyes, nose and a mouth, affections, passions; accordingly we find that in zoölogical classes all over the world the humble dogfish affords an invaluable epitome and ground-plan of human anatomy.

Men have been insulted by the implications of this fact and still more by the statement that man

Fig. 5. The Face of the Most Primitive Living Shark (after Garman).

For details see p. xiv.

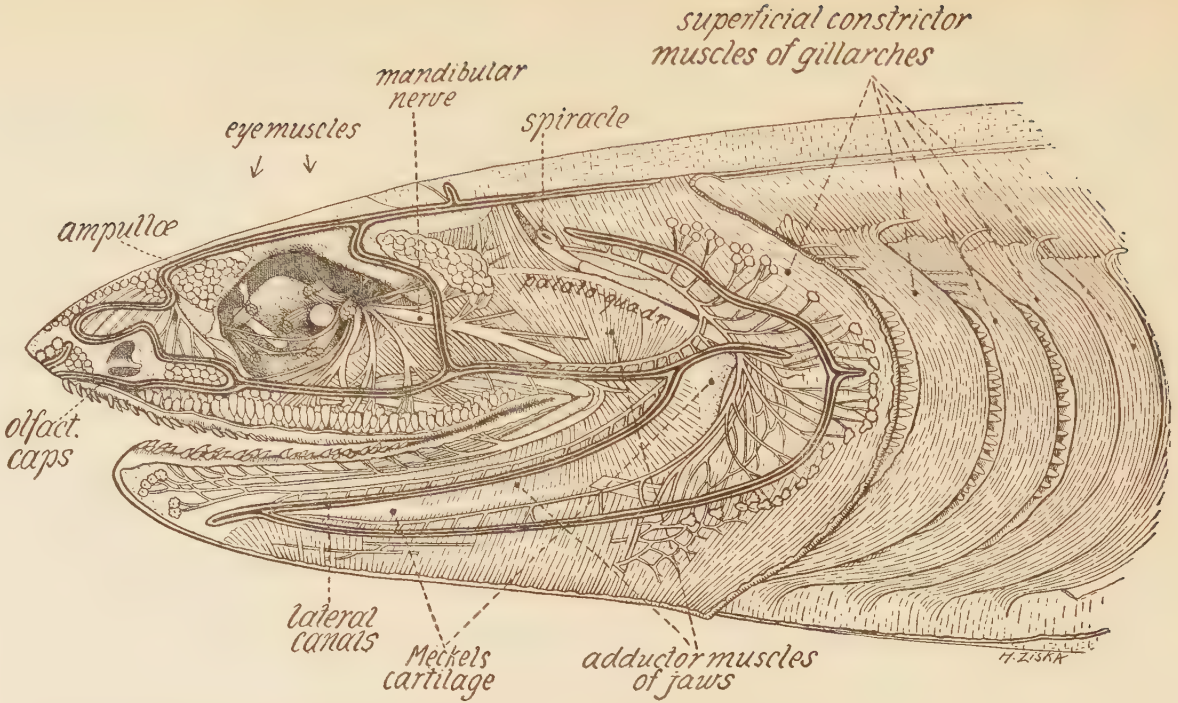

FIG. 6. INSTRUMENTS OF PRECISION IN THE HEAD OF A SHARK. (AFTER ALLIS.)
Lateral line canals black, bordered with white; nerves white; muscles streaked; cartilage stippled. For details, see p. xiv.

is far nearer in architectural plan to the shark than the latter is to whatever invertebrates we may choose to name as the starting-point of the whole vertebrate tree of life; but such are the secure judgments of comparative anatomy.

Much that might appear mysterious and inscrutable in the anatomy of the human face may reasonably be explained as a heritage from far-off shark-like ancestors, which human embryos also recall. Let us therefore look a little more closely into the construction and functioning of the face of this human prototype.

Always remembering that the face is merely the food-detecting and food-trapping mask in front of the brain, we find in the shark's apparently simple face a truly marvelous assemblage of instruments of precision (Fig. 6). First among these food-detecting devices rank the smelling organs, rosette-like membranes exposed in the olfactory capsules under the nostrils, capable of detecting chemically the very minute quantities of blood or other animal matter dissolved in sea water. These smelling capsules lead by prominent nerve tracts to the large forebrain, in which the smelling centers are the dominant elements (Fig. 81).

In the brain these olfactory messages stimulate the motor nerves controlling the eye muscles and other nerves controlling the locomotor muscles, in such a way that the shark turns and moves toward the source of the odor.

The eyes of a shark are fundamentally similar to those of a man but their marvelous intricacy forbids an attempt to discuss them in this brief space. Each eye is moved by six sets of eye muscles (Fig. 6), which turn the pupil toward the goal of movement.

As the food is reached and the stimulation of smell, sight and other senses reaches its climax, there is a convulsive expansion of the jaws, the food is torn by the jagged teeth, the jaws snap shut with the vicious force of a bear-trap, and the intense pleasure of swallowing the precious life-giving morsel is experienced.

Thoroughly equipped research laboratories could profitably occupy the time for decades to come with a study of what really happens when a shark detects its food and rushes forward to engulf it, for this apparently simple but in reality vastly complex sequence holds many secrets of vital importance to human beings.

However, the fact that even the true nature of nerve currents is as yet very imperfectly known does not prevent us from realizing the value of even a homely face to all animals that navigate the waters or move upon the land or in the air.

Not the least important of the shark's detecting and navigating instruments are the very numerous "ampullæ" that are so thickly scattered all over the surface of the head. Each of these pits is connected with a nerve tendril and thousands of these nerves run together into larger tracts, which finally run into the brain itself. Possibly these ampullæ detect vibrations of low frequency in the water and in some way coöperate with the olfactory nerves in giving stimuli proportional to the nearness of the source.

Then there are the taste organs scattered over the mouth cavity, all wired most carefully and elaborately and connected with the appropriate brain centers.

The so-called "internal ears" embedded in the cartilage on either side of the hindbrain, consist chiefly of the ingenious semi-circular canals (see pages 202–6, Fig. 104), arranged like our own in

three planes and capable of analyzing any movement of the body into three directional components.

These instruments of precision communicate their findings to the brain and form essential partners to the instruments carried by the face.

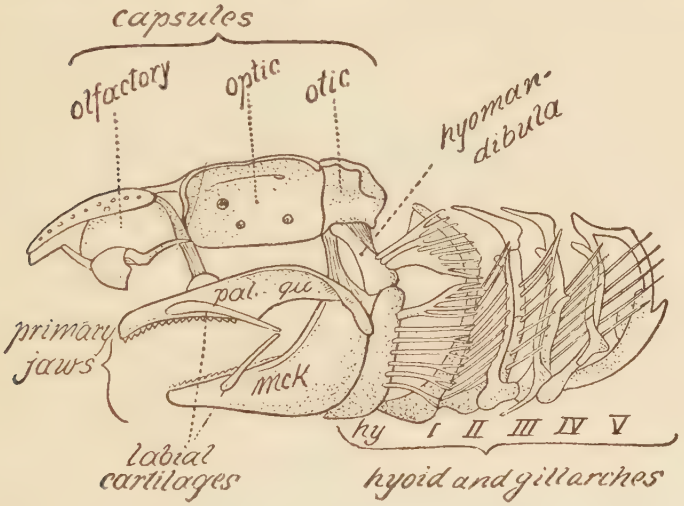

Fig. 7. Cartilaginous Skeleton of Head of Shark, Comprising Braincase, Primary Upper and Lower Jaws and Branchial Arches.

The scaffolding or skeleton of the face (Fig. 7) consists of three principal parts: first, the cartilaginous capsules (olfactory, optic, otic) that support the paired organs of smelling, sight and balancing; second, the cartilaginous trough and box that enclose the brain; third, the cartilaginous upper and lower jaw-bars (palatoquadrate, Meck-

el's cartilage), with certain connecting bars (hyomandibular, ceratohyal) that tie the jaws on to the braincase.

These jaw cartilages resemble the bars of cartilage (I–V) that form the supporting framework for the gills.

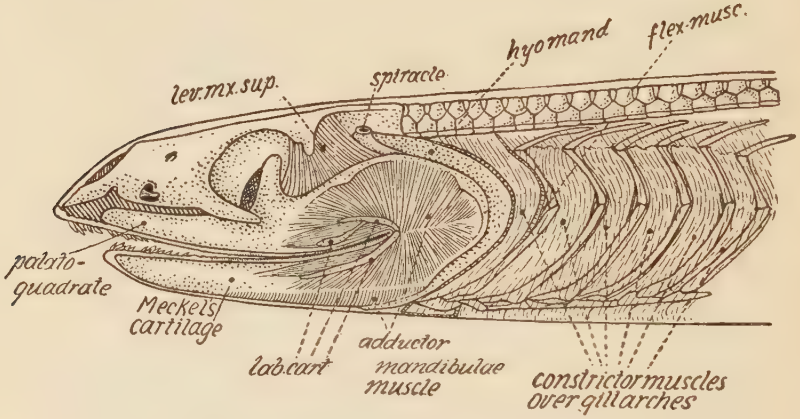

Fig. 8. Jaw Muscles of Shark, Showing the Essential Similarity of the Jaw Muscles to the Constrictors of the Branchial Arches.

For details, see p. xiv.

Even the jaw muscles appear to be modified gill-arch muscles. The principal jaw muscles (Fig. 8) are simply bands or sheets of muscle wrapped around the angular bend where the upper and lower jaw segments articulate with each other. The lower jaw is pulled downward chiefly by a backward pull of the horizontal muscles.

All these muscles, like those of the locomotor apparatus, are composed of striped muscle fibers and each little fiber is a sort of engine, deriving its fuel from the chemical glycogen in the blood and its explosive impulse from a tiny nerve fiber.

Over the whole of this great complex is stretched a tough but flexible envelope, the skin, which is studded with minute teeth, or shagreen.

Around the jaw-bars the shagreen gives rise to large teeth.

Thus in barest outline we have the elements of the face and its connections with the braincase in the shark. If we are fond of mysticism we will say that in the cramped brain-box lives the shark himself, who receives the multitudinous messages from his detecting instruments and shapes his actions accordingly. In this anthropocentric philosophy a shark's face is highly expressive of the shark's piratical and cruel character. If we wish to be thoroughly behavioristic, on the other hand, we will regard the shark's conduct as the automatic resultant of the various stimuli received by his sensorium, which were transmitted to the complex apparatus in the central nervous system, the office

of which in turn is to play off one stimulus against the other and to shape the motor responses into profitable combinations. In this case the shark's face is innocent of cruelty or piracy and is merely an assemblage of coördinated instruments of precision packed into the forepart of a vessel of appropriate streamline form.

At this place we do not have to discuss what brought about this marvelous aggregation of coördinated apparatus. All we need emphasize is that in the face of a shark a man may behold, as in a glass darkly, his own image.

Nevertheless a man should not flatter himself that he is a direct descendant of some powerful robber-baron such as the tiger-shark. Always in earlier times we have been only the little stealers of small fry and even when we attained the mammalian grade we were still specializing in capturing small living things.

THE MASK-FACE OF OUR GILLED ANCESTORS

A skull finds but little favor with the man in the street and possibly it would not interest him much to be told that every one of his twenty-eight skull bones has been inherited in an unbroken

Fig. 9. Cross-section of the Skull of a Fossil Ganoid Fish, Showing the Bone Cells (after Pander).

For details see p. xiv

succession from the air-breathing fishes of pre-Devonian times.

However, we wish to go even back of that and are curious to know why animals ever acquired a skull at all. The "basic patent" for the strengthening of all skeletal parts is the bone-cell, which invades both the skin covering the head, where it forms "derm bones," and the underlying cartilage or braincase; everywhere it deposits phosphate of lime and other salts, thereby greatly stiffening the skin and strengthening the brain-box.

The skull of all vertebrates above the sharks is a complex bony structure consisting of an outer shell, or dermocranium, originally derived from the many-layered skin, and an inner skull, or endocranium, derived from the cartilaginous brain-trough and its associated three pairs of capsules for the nose, eyes and inner ears.

The same kind of cells surround the elastic notochord or primitive axial rod, and deposit the bony tissue along certain tracts between the tough membranes that separate the muscle segments. In this way rods called ribs are produced as well as the bony arches above the notochord. All this results in a strong framework, which supports the

powerful body muscles that drive the body through the water.

The braincase is the thrust-block (Fig. 10) that receives the forward push from the backbone and

Fig. 10. The Wedge-shaped Braincase of a Fish, Acting as a Thrust-block or Fulcrum for the Backbone.

For details, see p. xiv.

the reaction from the water. The roofing bones over the braincase and the keel bone (parasphenoid) on the under side of the braincase together form a long wedge which is thrust forward into the water. To the sides of the skull are attached first,

Fig. 11. The Facial Armor and Jaws of a Devonian Lobe-finned Ganoid Fish (after Pander).

The skull seen from above. For details see p. xiv.

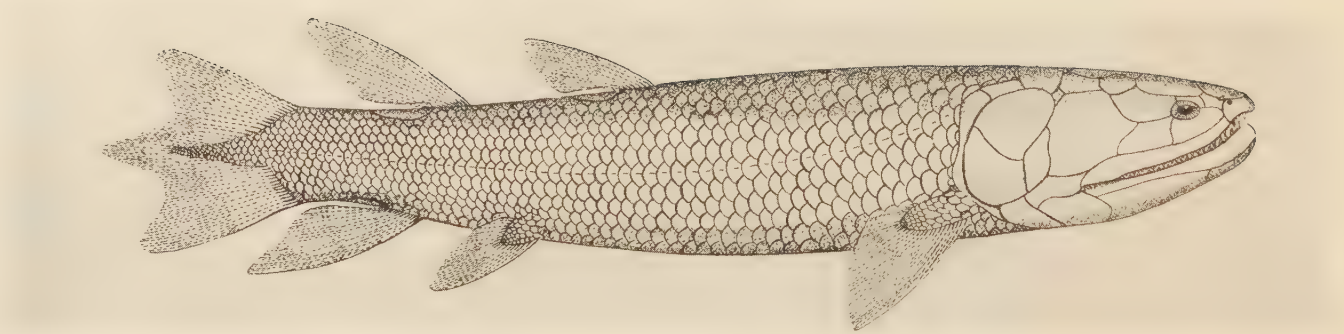

Fig. 12. First Claimant to the Line of Ancestry of the Higher Vertebrates. Devonian "Lobe-fin" (after Bryant).

For details see p. xv.

the complex jaws, consisting of the primary or originally cartilaginous upper and lower jaws plus their bony dermal covering, and second, the sliding bony covers of the gill chamber.

In the modern sharks the skeleton is stiffened by calcium carbonate rather than by phosphate of lime, the skin is stiffened chiefly by the shagreen or little teeth on its surface and the skeleton as a whole remains in a low stage of evolution.

On the other hand, in the ancient lobe-finned ganoid fishes, which stand much nearer to the direct line of human ascent than do the sharks, phosphate of lime is deposited by true bone-cells and the skull comprises a bony mask and a bony braincase as described above.

The whole surface of the mask (Fig. 11) is covered by a thin enamel-like layer, smooth and shining, called ganoine.

The jaws of the ancient ganoids, well covered both on the inner and outer sides by an armor of bony dermal plates, carried large sharp teeth with deeply infolded or labyrinthine bases (Fig. 18A).

There is every reason to regard these mail-clad robbers as lying not far off the main line of ascent. The alligator-gar of the lower Mississippi system,

although belonging to another order of ganoid fishes, bears a striking general resemblance to its Devonian relatives.

Among these ancient ganoid fishes there are two groups that have claims for the honor of standing nearest to the main line of ascent. The first lot were fierce, predatory, pike-like forms, which had stout fan-shaped paddles, two pairs, corresponding to the fore and hind limbs of land-living vertebrates. To judge from the fact that they had internal nares or nostrils as well as external ones, these ancient lobe-finned ganoids already possessed a lung in addition to gills and were therefore able to breathe atmospheric air directly when the streams and swamps in which they lived temporarily became dry. Today this group of lobe-finned or crossopterygian ganoids is represented, if at all, only by two living genera of fishes: the bichir (*Polypterus*) of the Nile and its elongate relative *Calamoichthys*. In its mode of embryonic development *Polypterus* shows resemblances both to the lung-fishes and to the Amphibia.

The rival claimants for the honor of standing in the human line of ascent were the true lung-fishes, or Dipnoi. The several survivors of this group at

Fig. 13. Second Claimant to the Line of Ancestry of the Higher Vertebrates. Devonian Dipnoan (after Pander).

For details see p. xv.

the present time, including the famous lung-fish (*Neoceratodus*) of Australia, all have very well-developed and functional lungs in addition to gills. Moreover, the embryonic development of the modern lung-fish, it has been shown, closely parallels that of certain existing salamanders.

Nevertheless, all the fossil and recent fishes of this dipnoan group had definitely and hopelessly removed themselves from the main line of ascent, since they had already either reduced or lost the marginal bones of the upper jaw and had developed peculiar and specialized fan-shaped cutting plates on the roof of the mouth and on the inner side of the lower jaw.

The earliest of the land-living or four-footed vertebrates, on the contrary, retained the marginal jaw bones and never developed the fan-shaped cutting plates on the roof of the mouth.

To make a long story short, the real ancestors of the higher vertebrates were probably neither true dipnoans, nor any of the Devonian lobe-finned ganoids, but were the still undiscovered common ancestors of these rather closely related groups living somewhere, perhaps in Lower Devonian or Upper Silurian times.

The evidence of embryology and comparative anatomy points unmistakably to the derivation of the land-living vertebrates from air-breathing fishes, with stout paired fore and hind paddles and a complex skull of the general type described above. The lobe-finned fishes as a whole appear to be

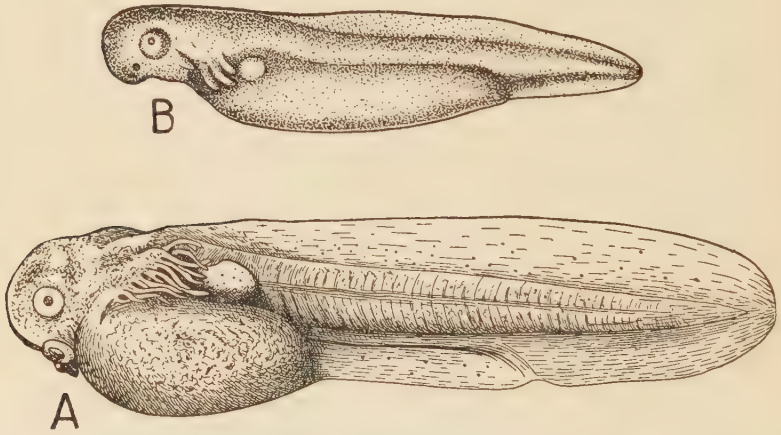

Fig. 14. Embryos of Modern Lobe-finned Fish (A) (after Budgett) and Amphibian (B) (after S. F. Clarke).

For details, see p. xv.

near to the direct line of ascent, although each of the known members of the group is probably too late in time and too specialized in certain details of skull structure to be the actual ancestor of the land-living vertebrates.

In view of the mobility and fleshiness of the human and other mammalian faces it may be

deemed surprising that one should seek to derive the higher vertebrates from fishes whose whole head and face were covered with a porcelain-like armor; but in the following pages we shall follow this amazing transformation step by step.

OUR ANCESTORS COME OUT OF THE WATER

Plant life is believed to have originated in the sea in early Archeozoic times. As far back as Devonian time it had succeeded after long ages of struggle in adapting itself to terrestrial life and there were great forests of low types of trees preceding the still greater swamps of the Coal age. No remains of amphibians have hitherto been found associated with Devonian plants, and the transformation of air-breathing fishes into lowly amphibians took place during the millions of years in which the fossil record of vertebrate life is still defective. But at the time of the formation of the older coal beds of Great Britain there were still surviving some very low types of amphibians which retained more of the fish-like characters in the skeleton than did any later forms known.

These highly interesting remains were imperfectly described by earlier authors but they have

been successfully restudied by Professor D. M. S. Watson of University College, London, in the light of his extensive knowledge of later fossil amphibians. Under his keen scrutiny these oldest known land vertebrates have yielded many facts of far-reaching significance. He has shown that in certain of these forms the shoulder-girdle was

FIG. 15. ONE OF THE MOST PRIMITIVE KNOWN AMPHIBIANS FROM THE LOWER CARBONIFEROUS OF ENGLAND (RESTORATION AFTER WATSON'S DATA).

For details, see p. xv.

still attached to the skull by a bony plate, as it is in typical fishes, and that the bony plates of the shoulder-girdle were still readily identifiable with those of fishes, whereas in later types these plates became highly modified.

The bony mask covering the face and braincase of these oldest tetrapods[1] is of the greatest interest in the present connection, for in it we find the starting-point for everyone of the twenty-eight

[1] A name often applied to the oldest four-footed land-living forms, both amphibians and reptiles.

Fig. 16. Skull of One of the Oldest Known Amphibians (*Loxomma allmani*).

After Embleton and Atthey.
A. Upper surface. B. Under side.

bones of the human skull, together with many other bony elements which were reduced and gradually eliminated in the long procession of forms from fish to man.

Before looking forward to man, let us look backward and see how the skulls of these earliest explorers of the land compared with those of their collateral ancestors, the air-breathing, lobe-finned ganoids.

The greatest change is seen in the region of the gill chamber, just behind the upper jaws. In the fish this was covered by a beautifully jointed series of bony plates, as perfectly articulated as any suit of armor ever made by man. In the oldest amphibians, however, these bony plates behind the jaws have disappeared completely, leaving an exposed area called the otic notch just behind the upper jaw. This is the region of the middle ear or sound-transmitting apparatus in modern amphibians and apparently these ancient amphibians had already acquired this new instrument of precision. In the lower jaw the bony plates covering the under surface of the throat had also disappeared. In the region above the nostrils the mosaic of small bones found in the lobe-finned

fishes had been replaced by two large bones henceforth traceable directly to the nasal bones of man. The several bony plates on the face surrounding the eye had also been changed in proportions.

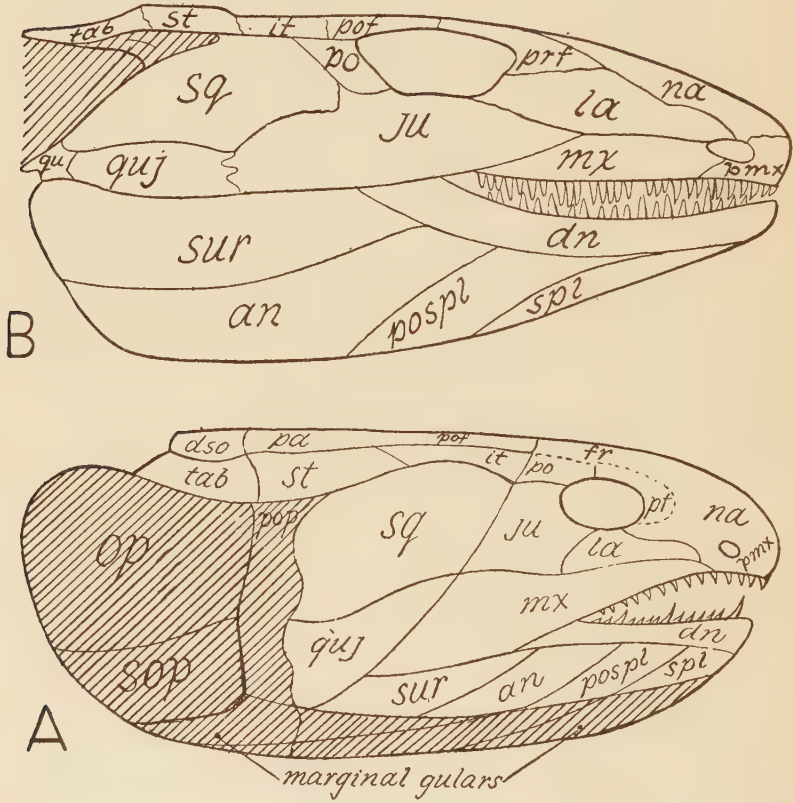

Fig. 17. Skulls of Lobe-finned Fish (A) and Early Amphibian (B), Showing Loss of Opercular Series in the Latter (A, after Traquair and Watson, B, after Watson).

In the primitive amphibians the space formerly covered by the opercular region was covered by the tympanum or drum membrane. For details, see p. xv.

On the other hand, many of the bony plates of the skull roof were taken over with little change by these oldest amphibians and the same is true of the derm bones of the lower jaw. On the under side of the skull (Fig. 53) the parasphenoid or keel bone had grown backward so as to cover the base of the braincase.

The teeth of the oldest amphibians were closely similar to those of the lobe-finned ganoids, both in general appearance and in microscopic structure. The porcelain-like outer layer of the skin bones covering the head of the lobe-finned fish had disappeared, leaving a rough surface. Thus the face of the oldest known amphibian, still consisting chiefly of a bony mask, was not as different from that of a lobe-finned fish as one might have expected.

Truly Nature's ways are not as man's ways. After producing a beautiful mask-face of great perfection and serviceableness, Nature started in to reduce and simplify it and eventually to cover up this mask with tender, sensitive flesh. From now on, the story of the human skull is the story of simplification and sacrifice of numbers, together with the refinement and constant differentiation of the elements that remained.

WHAT WE OWE TO THE EARLY REPTILES

The recent frogs, newts and salamanders, as every high school student knows, go through a fish-like or tadpole stage of development in the water and resort to this ancestral medium at the breeding season. The presence of fossilized gilled young of amphibians in the Coal ages shows that this water-breeding habit dates back very early in geological time and is in harmony with the origin of amphibians from swamp-living fishes. A great and revolutionary advance occurred when some daring amphibians succeeded in raising their eggs entirely on dry land, for thus arose the reptilian grade of organization and with it came the possibility of all higher forms of life, including man.

With regard to the bony face, the most primitive known reptile, *Seymouria*, has much in common with the older amphibians. It still retains the otic notch characteristic of the older forms and on its skull roof it preserves the full complement of small bony plates inherited from the amphibians and lobe-finned fishes. Also its outer upper jaw bones (maxillæ) still retain their primitive slenderness.

In the same age which yielded *Seymouria* (the

Permian of Texas) lived another, decidedly higher reptile, which had already acquired a significant resemblance to some of the lower mammal-like

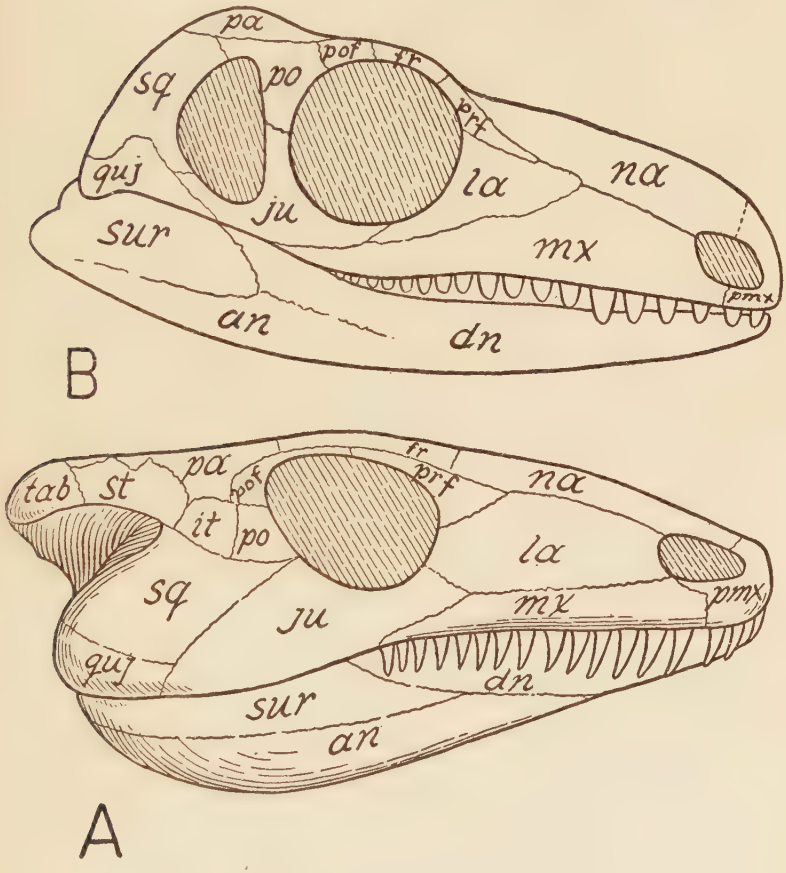

FIG. 19. TWO CRITICAL STAGES IN THE EARLY EVOLUTION OF THE SKULL.

A. Generalized reptile, retaining the full complement of amphibian skull elements. (After data of Broili, Watson, Williston.)

B. Primitive theromorph reptile, with reduced number of skull elements (after Williston). For details, see p. xvi.

reptiles of South Africa. This interesting form (*Mycterosaurus*) was carnivorous, like other progressive reptiles, but had not become too far specialized in this direction.

The most remarkable feature of its skull is a circular hole on the side of the skull behind the eye. This perforation in the bony mask of the temporal region was the first foreshadowing of the "temporal fossa" of the human skull.

As to the origin of this opening, studies on recent and fossil skulls of many kinds of reptiles indicate that the perforation arose through the progressive thinning of the bone, due to the absorbent action of the membranes surrounding the jaw muscle, which was attached to its inner surface. Meanwhile, in resistance to the stresses induced by the same muscle, the borders of the muscle area became strengthened into bony bars or ridges.

The bony tract below the temporal opening distinctly prophesied the mammalian zygomatic arch, the cheek bone of man.

Another progressive character of *Mycterosaurus* is the vertical growth of the upper jaw bone (maxilla), which up to that time had remained a shallow bar in front of the eyes. In the lower

jaw the principal tooth-bearing bone, or dentary, one on each side of the head, was relatively larger

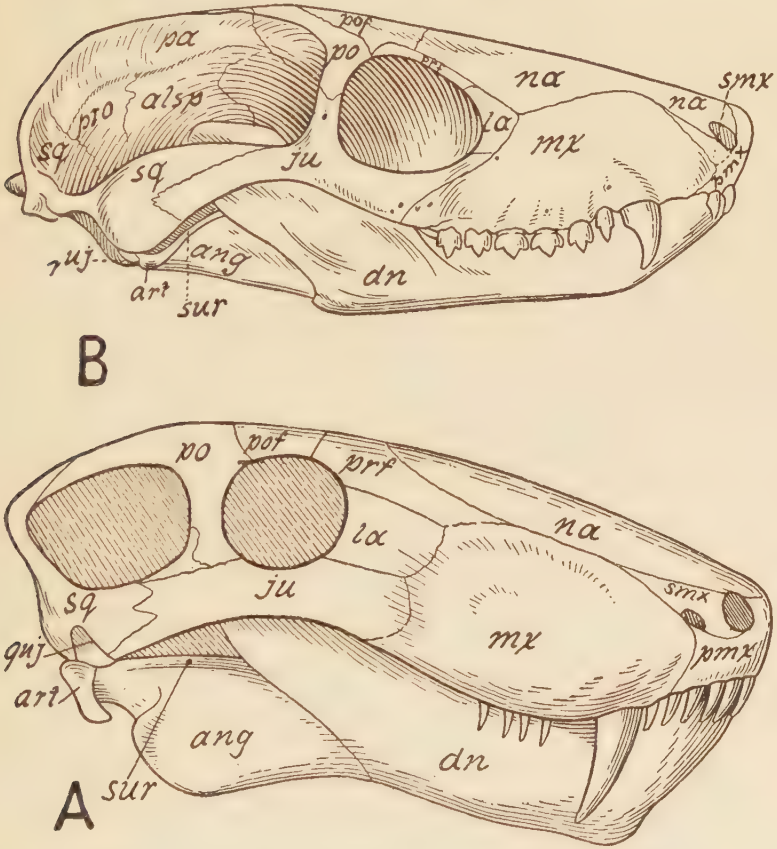

Fig. 20. Skulls of Earlier and Later Mammal-like Reptiles from South Africa.

(Data from Broom, Watson, Houghton.)
For details, see p. xvi.

as compared with the other bony plates of the jaw lying behind it, than it had been in earlier stages.

The next stage in the long ascent is found among the extinct mammal-like reptiles of the Karroo system of rocks in South Africa. Among these the lowest (Fig. 20A) are nearly as reptilian as lizards, while the highest (Fig. 20B) almost reach the mammalian grade of organization. The bony mask skull advances in various details toward the mammalian type especially in the modelling of the lower jaw, in the further development of a temporal fossa, or muscle opening, and of a cheek arch essentially of mammalian type.

THE ONE-PIECE JAW REPLACES THE COMPLEX TYPE

In later members of the series leading toward the mammals the dentary bone increased in size until it so far dominated over the elements behind it that finally they were crowded out entirely and the lower jaw of the adult thus came to consist solely of the two dentary bones (one on each side) connected at the front end, or symphysis. This result was fraught with momentous consequences for the further evolution of the bony face toward the human and other mammalian types.

Meanwhile the dentary bone (Fig. 21) by reason of its enlargement came eventually to press against

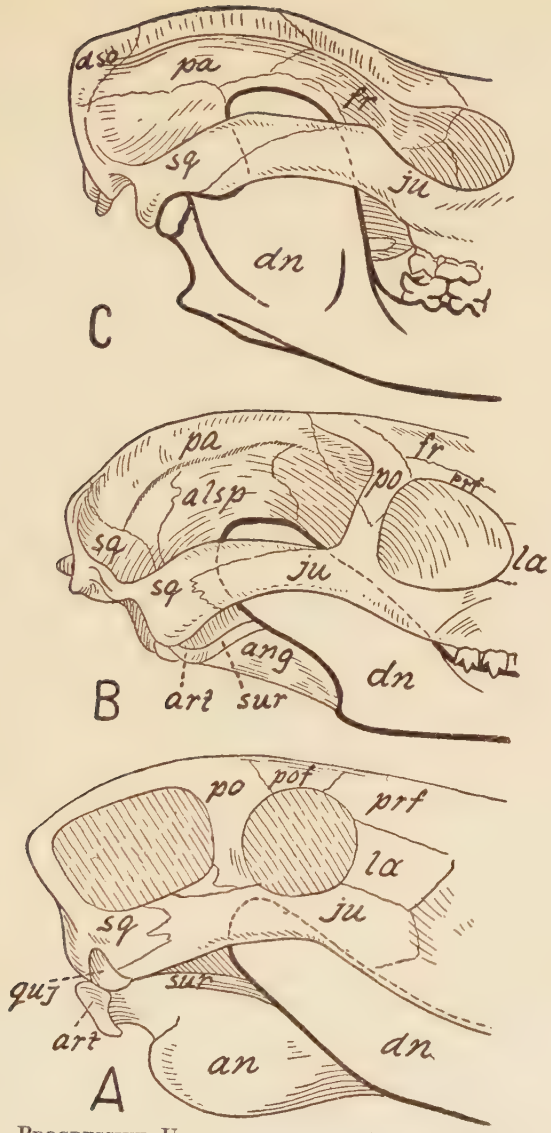

FIG. 21. PROGRESSIVE UPGROWTH OF THE DENTARY BONE OF THE LOWER JAW TO FORM A NEW JOINT WITH THE SKULL.

A. Primitive mammal-like reptile; B. Advanced mammal-like reptile; C. Primitive mammal.

For details, see p. xvi.

the very jaw muscles in which its upper end was embedded. In other cases when a muscle mass becomes subjected repeatedly to new pressures or friction across its line of action the surrounding

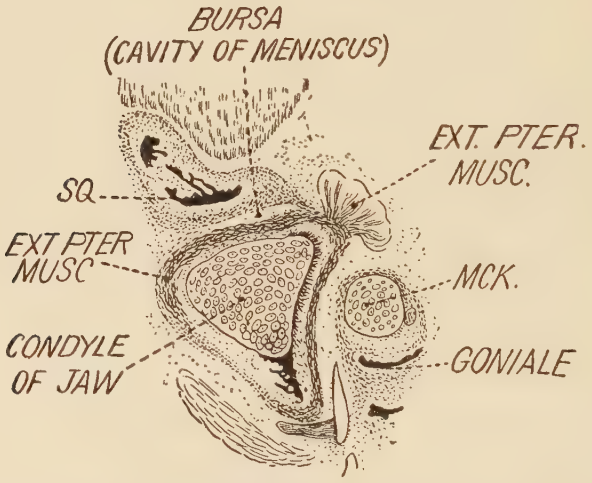

Fig. 22. Origin of the Interarticular Disc, or Meniscus, Lying Between the Lower Jaw and Its Socket in the Skull. (After Gaupp.)

membranes give rise to a cushion or sac of connective tissue filled with a clear liquid, which serves to prevent the opposing surfaces from grinding against each other. In an early embryo (Fig. 22) of a primitive mammal (*Perameles*) Professor E. Gaupp, the eminent comparative anatomist of Fribourg, found that a part of one

of the jaw muscles (the external pterygoid) during the course of its development passed between the lower jaw and its socket in the skull and there gave rise to the bursa or cushion (meniscus); this disc in all typical mammals prevents the lower jaw bone from grinding into its socket in the temporal (squamosal) bone.

In the immediate ancestors of the mammals the pressure of the dentary bone of the lower jaw transmitted through the meniscus or interarticular disc somehow resulted in the formation of a corresponding socket in the squamosal (temporal) bone of the skull.

Thus a new or mammalian joint was formed between the dentary bone of the lower jaw and the skull, while the old or reptilian joint, lying between the quadrate bone of the upper jaw and the articular bone of the lower jaw, was now greatly reduced in size, continued in the service of the middle ear and gave up its jaw-supporting function.

These great changes made possible all the new lines of evolution of the teeth that the mammals developed, which had never been possible for the reptiles; with these improved dental equipments the mammals soon overran the world, driving out

the reptiles and finally producing the primates, which eventually gave rise to man.

Thus the human face owes the fundamental plan of its upper and lower jaws to the mammal-like reptiles and earliest mammals in which these improvements were first worked out.

OUR MASK-FACE BECOMES MOBILE

The origin of the mammals is one of the most dramatic incidents in the whole story of human transformation from fish to man. The central problems set for the mammal-like reptiles were to speed up all their vital processes and to maintain them at a relatively high level; also to resist the extreme changes of temperature of the harsh, highly variable climates then prevalent, when periods of glaciation alternated with tropical heat. Means had to be found to insulate the body in slowly conducting substances so as to defy the cold; on the other hand, to enable the body to cool itself safely when over-heated. Reptiles have this power to a limited degree but it is greatly enhanced in the mammals. For this purpose many "basic patents" had to be worked out in the heat-conserving organs, in the circulation of body

fluids, in the breathing organs. The locomotor machinery was vastly improved, the brain and nervous system had to keep pace with the general advance and a new and much less wasteful method of reproduction had to be perfected.

Among the heat-regulating devices arising in the mammals, we note the following: (a) the diaphragm, a complex structure arising from the conjunction of various muscle layers of the neck and abdomen; it acts as a bellows to draw fresh air into the lungs and thus to increase the consumption of oxygen; the liberation of heat is a by-product; the glands in the skin multiplied and gave rise to (b) sebaceous glands, pouring out a wax-like substance that tends to keep the skin soft and pliable; (c) sudoriparous or sweat glands, lowering the body temperature by evaporation of the exuded moisture.

Chief among the heat-retaining structures was (d) the hair, which seems to have arisen from small tactile outgrowths of the skin. These at first grew out between the scales and later supplanted them. We do not know exactly when this substitution took place, as the skin of soft-skinned animals is very rarely, if ever, fossilized, but the later mam-

mal-like reptiles of the Triassic age were already so far advanced toward the mammalian grade that it would not be surprising if the initial stages in

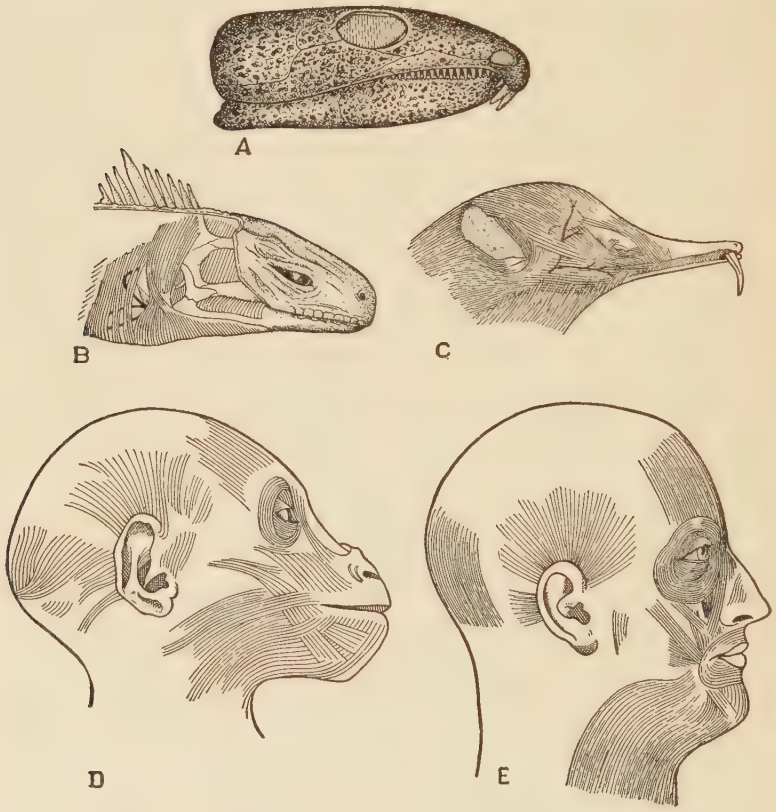

FIG. 23. ORIGIN OF THE FACIAL MUSCLES OF MAN.

A. Primitive reptile with continuous bony mask covering skull. The mask was covered with thick skin without muscles, as in the alligator. (After Williston.) B. Modern reptile with an open or fenestrated skull covered with thick, non-muscular skin. (From Fürbringer, modified from Ruge.) C. Primitive mammal in which the sphincter colli system has grown forward over the face. D. Gorilla. E. Man. (C, D and E after Ruge.)

For details, see p. xvii.

the formation of hair had already begun in them. At any rate, there is evidence that the bony mask of the earlier reptiles was already beginning to become leathery on its outer layer.

Even in the most primitive of living mammals the hard bony mask of the face has already begun to sink beneath the surface and a more or less pliable skin has been developed. But the most remarkable fact is that as the bony mask sank beneath the surface the "facial muscles," so characteristic of mammals alone among vertebrates, came into being. Where did they come from? In the reptiles the neck and throat are covered by a thin wide band of muscle called the primitive sphincter colli, which is activated by a branch of the seventh cranial nerve. In mammals this muscle, besides giving rise to the platysma muscle, has grown forward between the bony mask and the skin, along the sides and top of the face. As it grew forward over the cheek it sent out various subdivisions which either surrounded the eyes, or covered the forehead and cheeks, or surrounded the lips, or connected the lips with the cheeks, or were attached to the ears. Whenever the muscle mass sent forth a new branch it also sent into this

branch a twig from the main facial division of the seventh nerve (Fig. 24). Thus what are called the mimetic or facial muscles of mammals arose by the forward migration and subdivision of a muscle formerly covering the neck. For this doc-

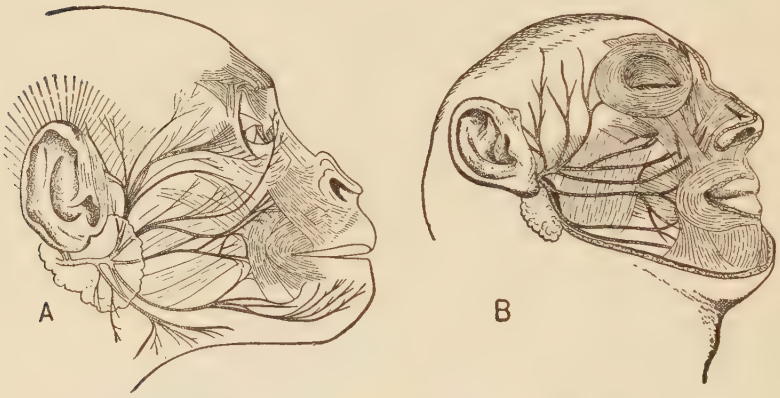

Fig. 24. Diagram Showing the Chief Branches of the Facial Nerve.

A. Gorilla. (After Ruge.) B. Man. (After Weisse.)

trine the anatomists Ruge and Huber have brought forward the most detailed and convincing evidence. Thus while mammals were exposed to cruel lacerations of the tender facial muscles, these same muscles became of great use in moving the lips, in closing the eyes, in moving the external ears and finally, in the apes and man, as a means of expressing emotion.

OUR LONG-SNOUTED ANCESTORS CROWD OUT THE DINOSAURS

For many millions of years during the Age of Reptiles the ancestral mammals enjoyed all the advantages of a higher level of vital activity, a higher body temperature, a better locomotor system, larger brains and more economical reproductive methods, which had made them far superior in grade to the group from which they sprang. Nevertheless, in all parts of the world where fossils have been found these advantages did not enable the mammals to supplant immediately their swarming relatives the reptiles. On the contrary, the reptilian class, which very early broke up into many orders, including the turtles, lizards, snakes, crocodilians, dinosaurs, birds, flying reptiles and many others, for millions of years dominated the earth, while both the mammals and the birds remained small and inconspicuous. For all the millions of years during which the dinosaurs ruled the land, the fossil record of life as it is preserved in Europe and North America so far reveals extremely few mammalian remains, and these only from very thin layers in widely separated parts of the world.

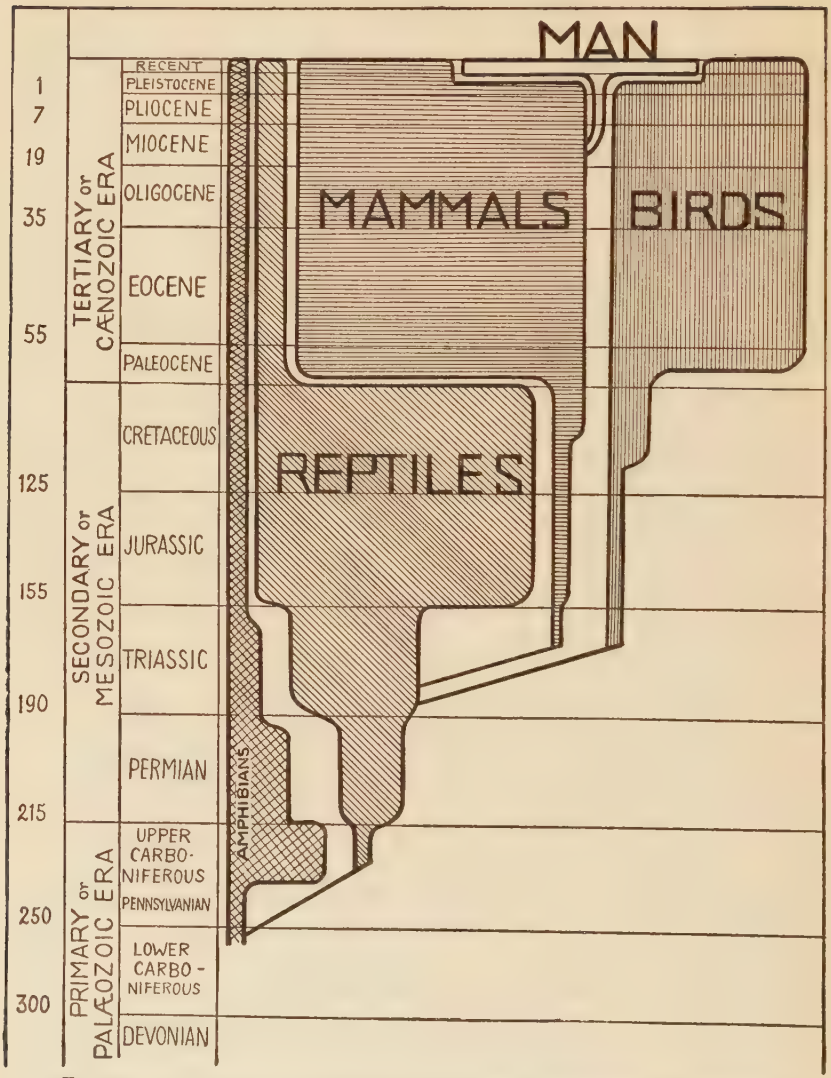

FIG. 25. SUCCESSIVE DOMINANCE OF THE AMPHIBIANS, REPTILES, MAMMALS AND BIRDS, MAN.

Numerals at left stand for millions of years since beginning of period, according to rate of "radium emanation" from uranium minerals, based on Barrell's estimates.

Fig. 26. The Common Opossum, a "Living Fossil" from the Age of Dinosaurs.

The known mammalian remains from these great formations consist mostly of very fragmentary jaws, with a few teeth in them, of tiny mammals. Most of these mammals were no bigger than mice, but in the closing stages of the Age of Reptiles a few of them became as large as beavers. Some of the mammals of the Age of Reptiles in Europe and North America are believed by certain authorities to be related to that most archaic of mammals, the egg-laying Platypus of Australia. Others seem to have been remotely related to the existing marsupials or pouched mammals, which today live chiefly in Australia.

The most primitive marsupial of today, however, is the common opossum of North America, which is one of our oldest "living fossils." It is, in fact, the little-changed descendant of a group of mammals that lived in the latter part of the Age of Reptiles. One of these ancestral opossums, represented by a fossil jaw and parts of the skull (Fig. 27), was found by Barnum Brown embedded beneath a large dinosaur skull in Upper Cretaceous rocks of Montana. This form, named *Eodelphis* (dawn-opossum) by Dr. W. D. Matthew, has the known jaw and skull parts so nearly like those of

its modern relative that we can actually fit the contours of the fossil opossum skull fragments into the skull of a recent opossum with very little adjustment of the latter; so that we may safely study the lowly 'possum as a representative and

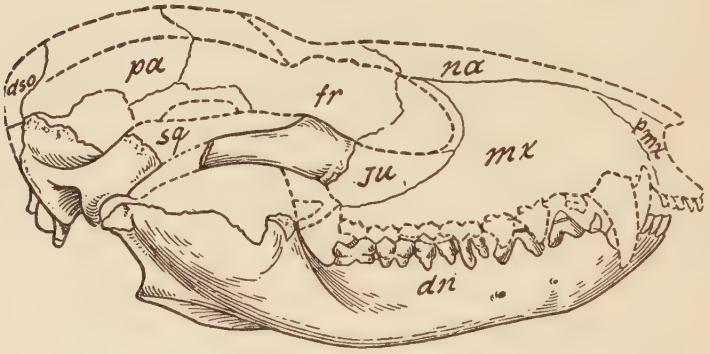

Fig. 27. Skull Parts of Extinct Opossum, Superposed on Outlines of Skull of Recent Opossum.

For details, see p. xvii.

descendant of the pouched mammals of the latter part of the Age of Reptiles.

Even the modern opossum skull is at first sight strangely similar to that of one of the mammal-like reptiles of the far-off Triassic. It will easily be seen from Fig. 28 that the opossum, like any primitive mammal, has inherited the entire ground-plan of its skull from its progressive reptilian ancestor. Considering the great advance in gen-

eral grade of organization described above, it is surprising that in the side view of the skull the

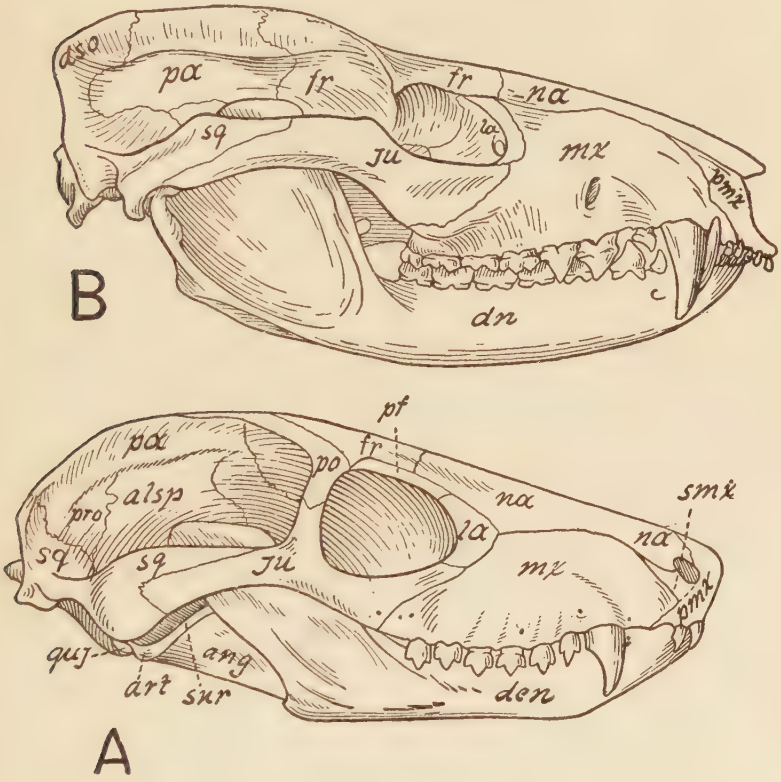

FIG. 28. SKULLS OF (A) ADVANCED MAMMAL-LIKE REPTILE AND (B) MODERN OPOSSUM.

For details, see p. xvii.

higher structural level of the opossum is indicated chiefly by the few conspicuous features figured below (Figs. 48–52). The jaw muscles of the opossum now cover the parietal and part of the

frontal bones, whereas in the earliest stages they lay beneath these bones.

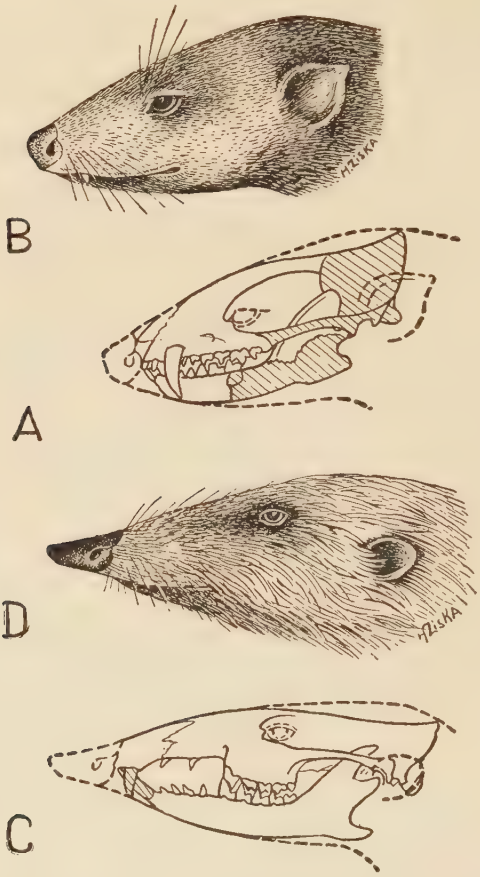

Fig. 29. Long-snouted Relatives of Ours from the Cretaceous of Mongolia. (Restorations.)

For details, see pp. xvii., xviii.

It has been explained above how this shift in relations began, by the overlapping of the edges

of these bones by the jaw muscles, which finally crept over and completely submerged the bone. Thus by the time we reach the primitive mammal stage of evolution almost the entire bony mask, which had originated as the bony skin on the surface, is now found covered by the facial and jaw muscles.

The relatives of the opossum and other primitive pouched mammals until several years ago were the only mammals of Cretaceous times of which anything definite was known as to their skull structure. In 1924 and 1925, however, Roy C. Andrews and his colleagues of the American Museum of Natural History discovered in the Cretaceous formation of Mongolia half a dozen imperfectly preserved skulls which appear to represent the forerunners of the higher or placental mammals (see also Fig. 77 iv below). These little skulls, which have been described by the present writer with the collaboration of Dr. G. G. Simpson, bring strong evidence for the conclusions of Huxley, Henry Fairfield Osborn, Max Weber, W. D. Matthew and others that the remote ancestors of the placental or higher mammals of the Age of Mammals were small insectivorous

animals with sharp cusps and blades on their tritubercular or triangular upper molar teeth. In these little Cretaceous placentals the skull and teeth were in many ways like those of certain existing insectivorous mammals, such as the tenrec of Madagascar.

All the evidence available from several sources indicates that the remote ancestors of the line leading to all the higher mammals, including man, were small long-snouted mammals, of insectivorous habits and not unlike some of the smaller opossums and insectivores in the general appearance of the head.

BETTER FACES COME IN WITH LIFE IN THE TREE-TOPS

Immediately upon the close of the Age of Reptiles the mammals appear in certain regions in North America and Europe in great numbers and variety. Palæontologists think it probable that they came from Asia, possibly by way of the Behring Straits land-bridge. In the Basal Eocene or Paleocene rocks of New Mexico and a few other places have been found thousands of fragments of fossilized jaws and teeth and several incomplete skeletons of mammals, ranging in size from mice

FIG. 30. THE PEN-TAILED TREE-SHREW OF BORNEO.

A "living fossil" representing a little-modified survivor of the Cretaceous ancestors of the Primates. (Based on photographs and data given by Le Gros Clark.)

Fig. 31. The Spectral Tarsier of Borneo.

A highly specialized modern survivor of a diversified group of Primates that lived in the Lower Eocene epoch over fifty million years ago. (Data from specimen and photograph by H. C. Raven.)

to large badgers. These belong mostly to wholly extinct families of placental mammals, usually with very small brains and teeth variously adapted for eating insects, flesh or vegetation.

In the Basal Eocene formation of Montana have been found teeth and bits of jaws of mammals that apparently were somewhat nearer to the line of human ascent. One lot of teeth and jaws appear to be related remotely to the existing tree-shrews of the Indo-Malayan region. These little animals in many ways approach the lowest of the Primates, especially in the construction of the skull and teeth.

The second lot of teeth from the Basal Eocene of Montana are judged by Dr. Gidley of the U. S. National Museum to be related distantly to the existing tarsier of Borneo and the Philippine Islands. These very curiously specialized nocturnal primates (Fig. 31) have enormous eyes, large but simple brains, very short noses and very long hind legs, upon which they hop about among the trees. In brief, the tarsier family appears to be one of those numerous groups that after attaining a high level of general organization at a relatively early period, start off on an extremely

specialized side line and thus remove themselves from the direct line of ascent to higher forms.

Much more conservative and central in structural type are the fossil primates of the extinct family Notharctidæ from the Eocene of Wyoming and New Mexico. The fossil skeletons of these animals (Fig. 32) have grasping hands and feet of the tree-living type preserved in the modern lemurs of Madagascar. The same is true of the feet of the extinct lemuroid primates of the family Adapidæ from the Eocene of Europe.

Comparative anatomical and palæontological evidence unite to support the view that all the primates first went through an arboreal stage, some of them afterward coming down to the ground and carrying with them many of the structural "patents" acquired during their long schooling in the trees.

The hind foot of all known fossil and recent primates below man is of the tree-grasping type with a divergent great toe and there is no substantial doubt, after the exhaustive critical discussions of this subject by Gregory (1916, 1921, 1927), Miller (1920), Keith (1923), Schultz (1924), Morton (1924, 1927) and others, that the whole order was from its first appearance primarily tree-living

FIG. 32. SKELETON OF A PRIMITIVE FOSSIL PRIMATE FROM THE EOCENE OF WYOMING (AFTER GREGORY).

For details see p. xviii.

in habit and that the foot of man has been derived from a grasping type with a divergent great toe.

Tree-living, possibly combined with nocturnal habits, favored the evolution of keen sight, and in the oldest known skulls of primates, from the

FIG. 33. SKULL OF A PRIMITIVE PRIMATE OF THE EOCENE EPOCH (AFTER GREGORY).

For details, see p. xviii.

Eocene perhaps fifty million years ago, we find the eye orbits already larger and better defined than those of contemporary terrestrial mammals.

The skull of one of the best known members of this group is drawn in Fig. 33, from fossil specimens in the American Museum of Natural History. In this form the chief advance beyond the primitive mammalian type (Fig. 27) is seen in the increase in the size of the eyes and the beginning of the

shifting of the eyes toward the front of the head. The muzzle, or olfactory chamber, is not yet reduced.

The still surviving primates afford a remarkably well graded series of faces, from the fox-like face of *Lemur* (Fig. 34A) to the quaint old-man-like faces of some of the Old World monkeys (Fig. 34C). In the lower forms (*Lemur*, etc.) a rhinarium, or moist patch, is present at the tip of the long snout, the opposite lips are separated by a notch in the mid-line and lack the mobility seen in the higher forms. In the latter, with the shortening of the muzzle, the rhinarium gives place to a true nose, the mucous-secreting skin being limited to the inner side of the nostrils and the nose eventually growing out between the nostrils. Meanwhile the opposite upper lips have become more broadly joined at the mid-line and finally the lips become highly protrusile through the constricting action of the strong orbicularis oris muscle.

In the New World, or platyrrhine, monkeys (Fig. 34B), which appear to represent an independent offshoot from some primitive tarsioid stock, the nostrils are widely separated, opening outwardly on each side of the broad median part of

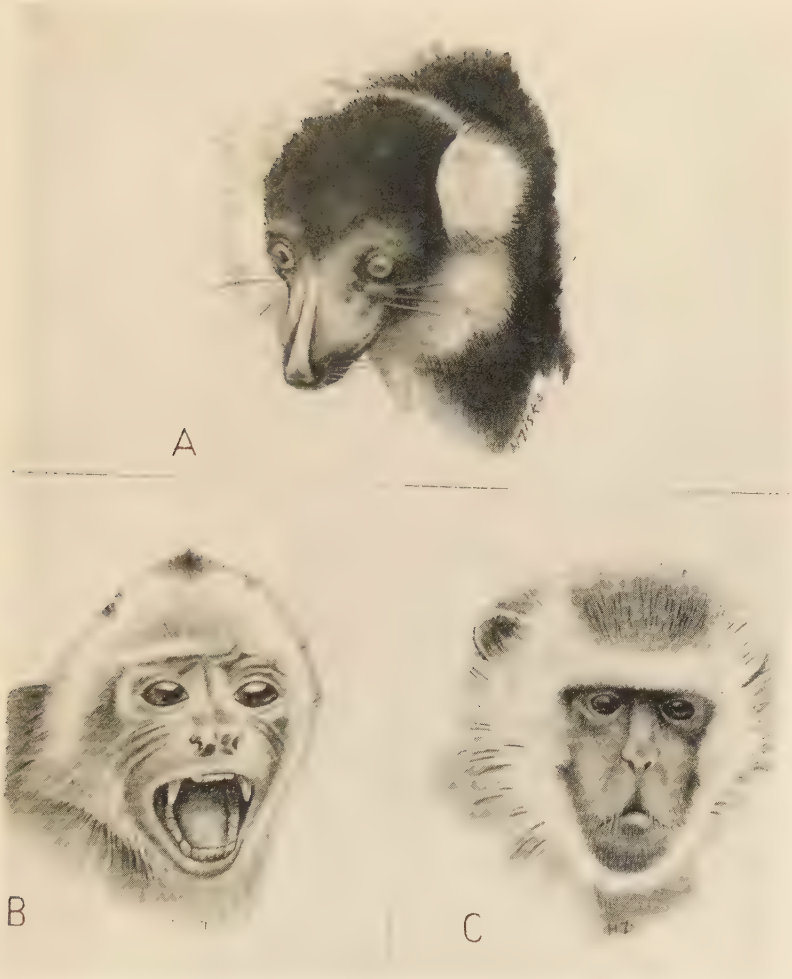

Fig. 34. Ascending Grades of Faces in the Lower Primates (after Elliot).

A. Lemur; B. South American monkey; C. Old World monkey.

For details see p. xviii.

the nose. In the Old World, or catarrhine series (including the monkeys, apes and man), the nostrils are drawn downward and inward toward the mid-line, so that they tend to make a V, with the tip pointing downward. The subsequent history of the nose and lips will be considered below (pages 129, 153).

The external ears of the lower primates also show many gradations from a more ordinary mammalian type (see below, pages 211–213) to the man-like ears of the chimpanzee and gorilla.

The habit of living either in trees or in a forested region, in so far as it afforded opportunities for securing insects, buds, tender shoots and fruits, made possible the various lines of evolution of the teeth which we observe in studying the fossil and recent primates. In the earliest forms the dentition as a whole retains clearer traces of an earlier insectivorous stage, with triangular sharp-cusped upper molar teeth. In the anthropoid the habit of eating tender shoots and buds is reflected in the molar teeth, which now have broad crowns with low-ridged cusps. The human dentition, while secondarily adapted for a more varied diet, still bears many indubitable traces of its derivation

from a primitive anthropoid stage like that of the fossil apes *Dryopithecus* and *Sivapithecus*.

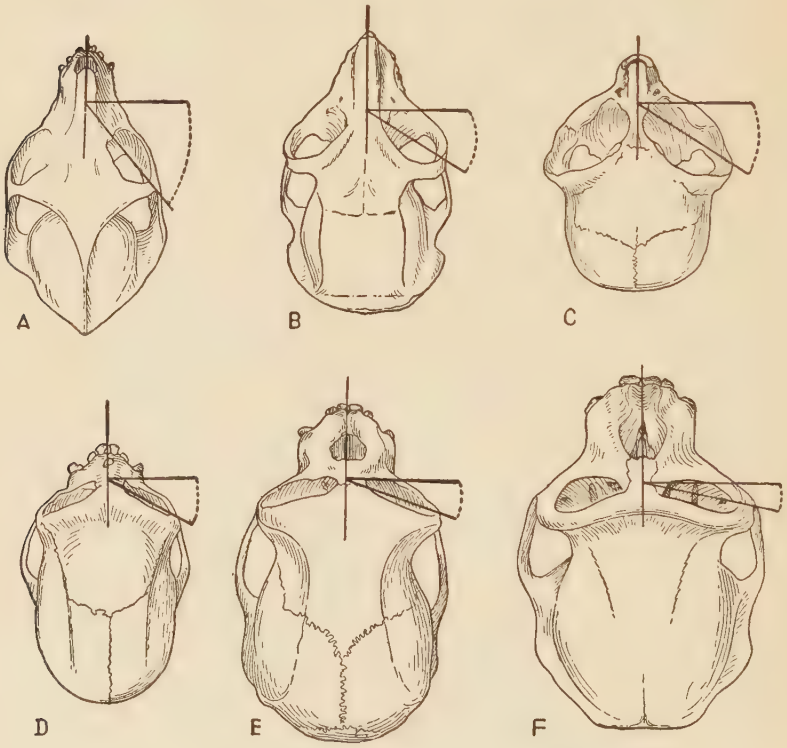

Fig. 35. Top View of the Skull in Representatives of Six Families of Primates, Showing the More Forward Direction of the Orbits in the Higher Forms.

A. Fossil lemuroid; B. African lemur; C. Tarsier; D. Marmoset; E. Gibbon; F. Chimpanzee.
For details, see pp. xviii, xix.

In some of the existing lemurs of Madagascar that retain the fox-like muzzle with its large smelling chamber, the eyes are less enlarged and look

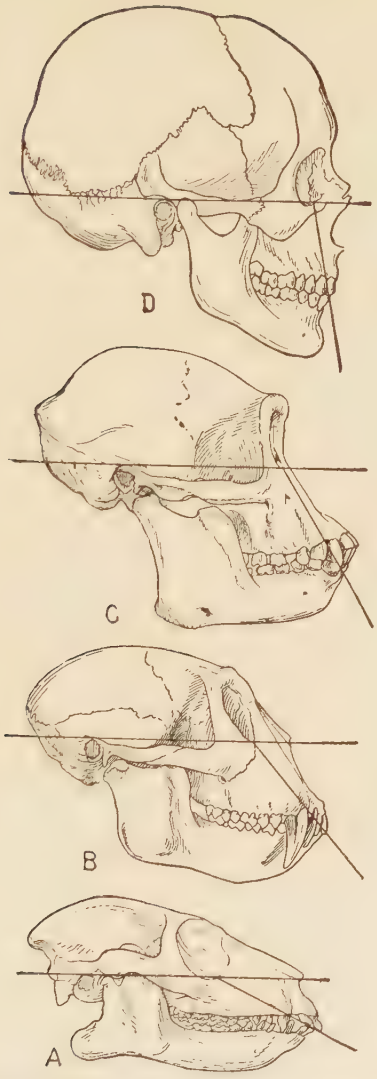

FIG. 36. SIDE VIEW OF SKULLS OF PRIMATES, SHOWING PROGRESSIVE SHORTENING OF THE MUZZLE, DOWNWARD BENDING OF THE FACE BELOW THE EYES AND FORWARD GROWTH OF THE CHIN.

A. Eocene lemuroid; B. Old World monkey; C. Female chimpanzee, D. Man. (B and C after Elliot.) For details, see p. xix.

partly outward as well as forward. But in all the more advanced lemuroids the eyes are larger, with more or less protruding orbits which tend to shift forward, finally restricting greatly the interorbital space and nasal chamber. This process culminates in the nocturnal galagos and in *Tarsius* (Fig. 31), in which the eyes are enormous and the eyes themselves are directed forward, although the orbits are directed obliquely outward.

In none of the lower primates, however, are the bony orbits directed fully forward and in none of them are the upper jaws prolonged downward beneath the eyes, as they are in the monkeys, apes and man.

The families of man, apes, monkeys, tarsioids, lemurs and tree-shrews are exceedingly rare as fossils except in a few localities and geologic horizons and the known remains usually consist chiefly of broken jaws with a few teeth. Nevertheless these fossils are of high value when studied together with the manifold families, genera and species of primates still living. In a series of publications beginning in 1910 I have shown how fully these recent and fossil forms, from tree-shrews to man, reveal the structural stages in the

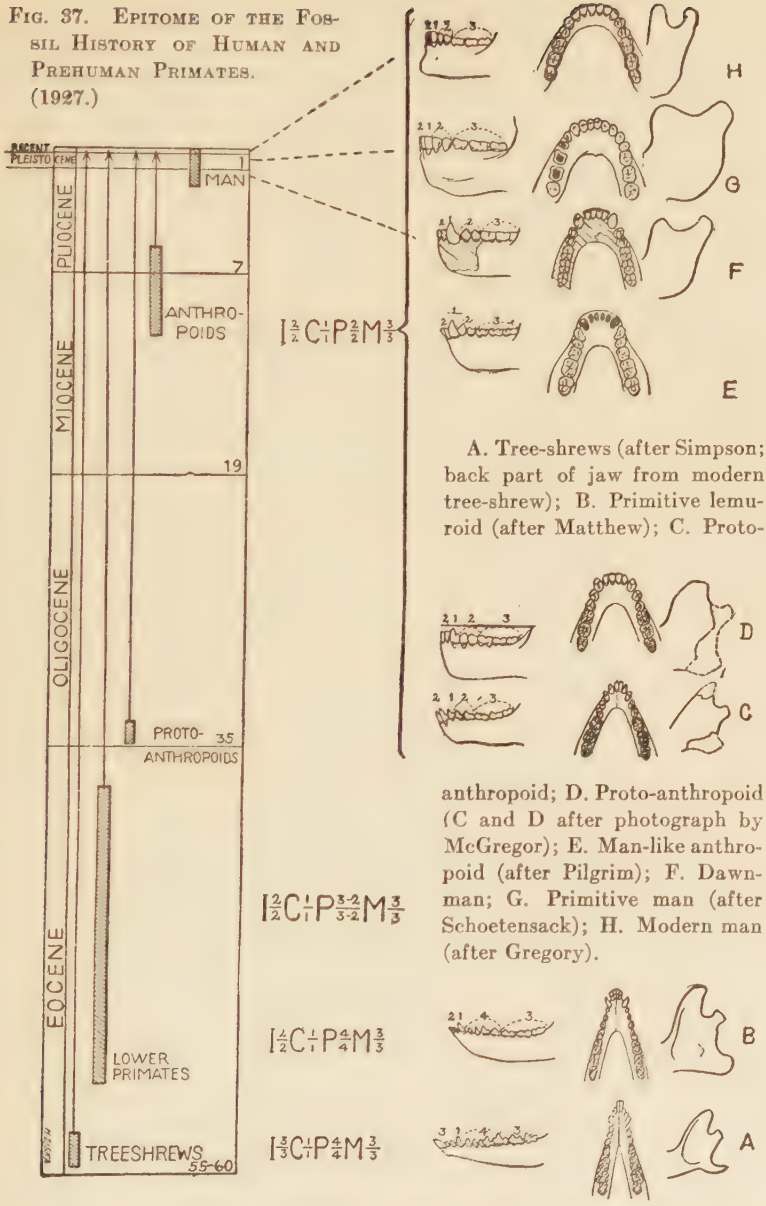

Fig. 37. Epitome of the Fossil History of Human and Prehuman Primates. (1927.)

A. Tree-shrews (after Simpson; back part of jaw from modern tree-shrew); B. Primitive lemuroid (after Matthew); C. Proto-anthropoid; D. Proto-anthropoid (C and D after photograph by McGregor); E. Man-like anthropoid (after Pilgrim); F. Dawn-man; G. Primitive man (after Schoetensack); H. Modern man (after Gregory).

The figures on the right give the estimated duration of time in millions of years since the beginning of each epoch. For details, see pp. xix, xx.

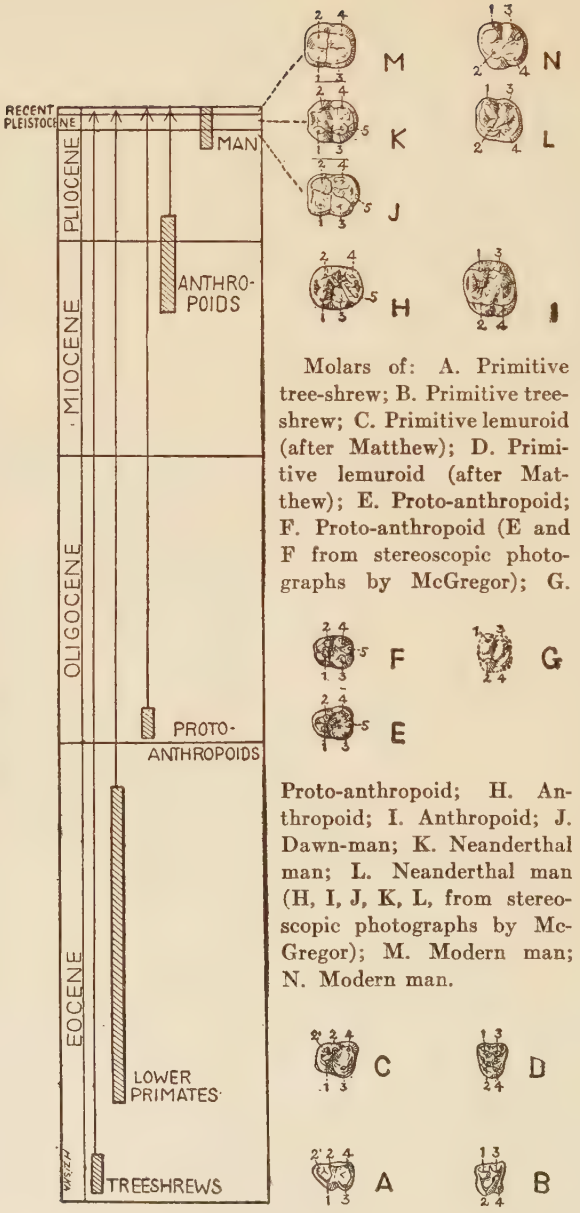

FIG. 38. EPITOME OF THE FOSSIL HISTORY OF HUMAN AND PREHUMAN PRIMATES (*Continued*).

Molars of: A. Primitive tree-shrew; B. Primitive tree-shrew; C. Primitive lemuroid (after Matthew); D. Primitive lemuroid (after Matthew); E. Proto-anthropoid; F. Proto-anthropoid (E and F from stereoscopic photographs by McGregor); G. Proto-anthropoid; H. Anthropoid; I. Anthropoid; J. Dawn-man; K. Neanderthal man; L. Neanderthal man (H, I, J, K, L, from stereoscopic photographs by McGregor); M. Modern man; N. Modern man.

For details, see pp. xx, xxi.

evolution of the teeth, jaws, braincase, middle and inner ear, vertebral column, pelvis, hands and feet.

Meanwhile Elliot Smith, Tilney, Hunter, Le Gros Clark and others have shown how the existing tree-shrews, lemurs, monkeys, apes and man present a progressive series in the evolution of the brain as a whole and of the various nuclei and centers controlling bodily functions and behavior.

Sir Arthur Keith and others have also traced step by step the structural adjustments in the diaphragm, abdomen and pelvic floor, as the originally horizontal body assumes a sitting position or moves erect as in the gibbon and man.

It is remarkable how completely the results of the students of the nervous system and of the anatomy of the viscera accord with studies on the evolution of the teeth, skull, limbs, etc., and on the classification and fossil history of the families and genera of Primates.

Taken together, these results afford cumulative evidence for the conclusions that man still bears in his whole organization an indelible stamp of the

tree-living habits of his remote primate ancestors and that these tree-living adaptations were overlaid by a later but very extended series of adaptations for bipedal running on the ground.

THE ALMOST HUMAN FACE APPEARS

Doubtless many factors conditioned the progressive enlargement and differentiation of the brain, which is so marked a characteristic of the whole Primate order, but perhaps the leading factor was the correlated use of eyes and hands and at first, feet, not only in locomotion but in the seizure and manipulation of food. And no doubt the habit of sitting upright also tended to free the hands for the examination of nearby objects, while the habit of climbing in an erect posture, as in the gibbon, finally gave rise to the almost human face of the anthropoid apes, as will presently be shown.

We do not yet know the exact time and place in which certain advanced primates began to take on specifically human characters, although there is much evidence at hand indicating that the time was not much earlier than the Lower Miocene, and the place somewhere within the known area

Fig. 39. One of Our Nearest Living Relatives. Female Chimpanzee and Young.

(From "Almost Human," by R. M. Yerkes. Courtesy of the author and The Century Company).

For details see p. xxi.

Fig. 40. Male and Female Chimpanzees.
(After J. A. Allen, from photographs by Herbert Lang.)

of the anthropoid stock at that time, which ranged from India to Spain. But Darwin's conclusion that mankind represents a peculiar and specialized offshoot from the anthropomorphous subgroup of Old World primates, after three-quarters of a century of anatomical and palæontological research, is backed by a mountain of evidence.

The female chimpanzee in the side view of the skull stands nearer in resemblance to man than it does to the primitive Eocene primate *Notharctus*. The chimpanzee in fact has acquired all the "basic patents" in skull architecture which were prerequisite for the final development of the human skull.

The most eminent students of the brains of animals and men conclude that partly as a result of the necessity for keen sight in actively climbing animals, the eyes in primates (Fig. 35) moved around from the sides of the face, where they are in the lower vertebrates, and were brought to the front, where in the anthropoid apes they finally acquired biconjugate movements and stereoscopic vision. In the anthropoid apes, moreover, the sense of smell no longer dominates the brain system as it did in lower vertebrates, but its reign

is usurped by the sense of sight. Concomitantly, the brain of the chimpanzee has increased greatly so that the braincase is distinctly subhuman in appearance. The erect position assumed by apes that climb so much by means of their arms as do the anthropoids has conditioned the bending downward of the face upon the braincase (Fig. 36).

Everyone recognizes in the chimpanzee (Fig. 40) a gross caricature of the human face, in which the mouth and lips are absurdly large and the nose flat with little or no bridge. But from the anthropoid viewpoint the human face may well appear equally grotesque, with its weak little mouth, exposed lips and unpleasantly protruding nose. Possibly the common ancestor of man and apes would be shocked by each of his descendants. But allowing for much divergent evolution in the end forms, what makes men and anthropoids so much more like each other in fundamental features of the face than either is to the oldest forerunners of the entire order, long antedating their nearer common ancestor? First, let us set down in parallel columns a few of these resemblances and differences.

FIG. 41. LEFT LOWER CHEEK TEETH OF FOSSIL ANTHROPOID (B) FROM INDIA AND FOSSIL PRIMITIVE MAN (A) FROM PILTDOWN, ENGLAND.

(A, from photograph by J. H. McGregor; B, after Gregory and Hellman).

The lower molars of the Piltdown jaw, although much ground down by wear, show the pure "*Dryopithecus* pattern" characteristic of recent and fossil apes.

For details see p. xxi.

	EARLIER PRIMATES (Cf. Figs. 33, 34A, 35A, 36A)	ANTHROPOIDS AND PRIMITIVE MAN (Cf. Figs. 35E, F, 42, 43, 44)
Muzzle and snout	Long, pointed, extended chiefly forward	Short, wide, extended chiefly downward
Mouth	Narrow, elongate	Wide, short
Tongue	Narrow	Broad
Lips	Not protrusile	Strongly protrusile
Number of premolars, upper	Four	Two
Number of premolars, lower	Four	Two
Form of first and second upper molars	Triangular, three main cusps	Quadrangular, four main cusps
Cusps of lower molars	Sharp	Low, blunt
Lower jaw	Long, slender	Short, deep
Opposite halves of lower jaw	Separate	Fused in front
Eyes	Look outward and forward	Look forward, binocular, biconjugate
Bony partition behind eye orbits	Barely begun	Complete
Premaxilla and maxilla	Separate	Fused in adult
Occipital condyles	On rear of brain base	More on under side of brain base

This comparison could be greatly extended by the inclusion of technical anatomical details, but is sufficient to indicate the main features of the bony face in which man and the anthropoids have advanced beyond the primitive primates. In the earliest primates the characters mentioned above are already adapted to a diet of insects and vege-

tation and to a horizontal position of the vertebral column; the anthropoids, on the other hand, are chiefly frugivorous and their vertebral column is more or less erect.

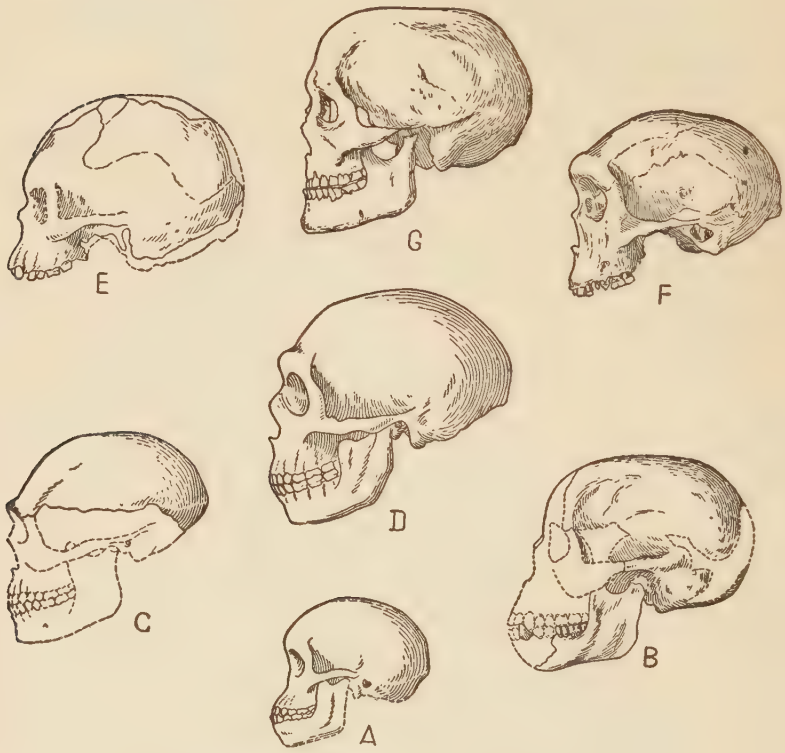

Fig. 42. Fossil Anthropoid and Human Skulls.

A. *Australopithecus*, a young extinct anthropoid (after Dart); B. *Eoanthropus* (after A. S. Woodward and J. H. McGregor); C. *Pithecanthropus erectus* (after Dubois); D. Neanderthal (after Boule); E. Talgai (after S. A. Smith); F. Rhodesian (after A. S. Woodward); G. Cro-Magnon (after Verneau).

In the female and young skulls the brow ridges are less projecting or entirely lacking. For details, see pp. xxi, xxii.

The close anatomical relationship of man to the anthropoids, together with the fundamental iden-

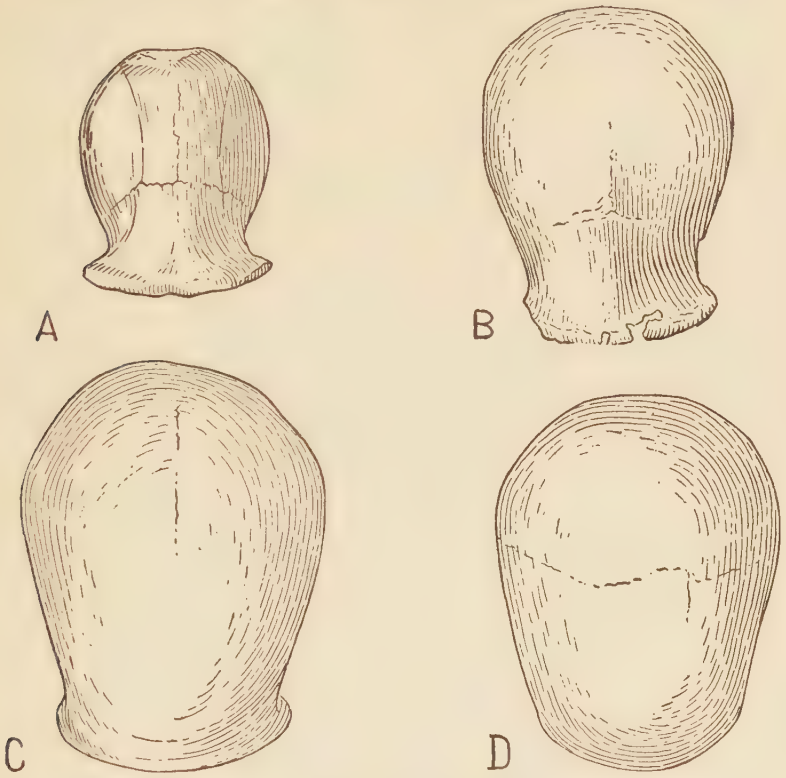

Fig. 43. Anthropoid and Human Skulls. Top View.

A. Chimpanzee (after Boule); B. *Pithecanthropus* (after Dubois); C. Neanderthal (after Boule); D. Cro-Magnon (after Boule).

tity in the molar patterns (Fig. 41) of the most ancient fossil men to those of still older anthropoids, indicates that man has been derived from frugivorous pro-anthropoids and that after man

left or had been driven forth from the ancient forests, his omnivorous-carnivorous habits were developed during the age-long and bitter struggle for life on the plains. Thus the gentle pro-anthropoids, quiet feeders on the abundant fruits of the forest, introduced a long period of peaceful development in the strenuous upward struggle.

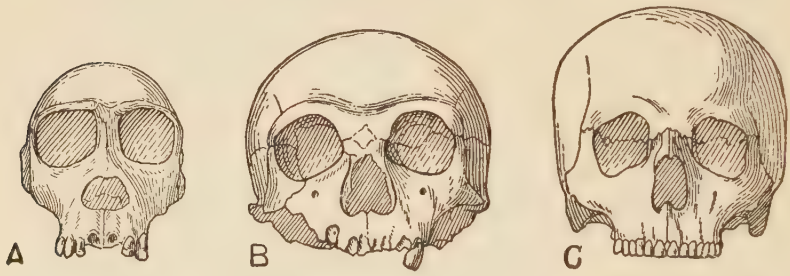

Fig. 44. Anthropoid and Human Skulls (after Boule).
A. Chimpanzee; B. Neanderthal; C. Modern European.

This peace was rudely broken when from some zoological Garden of Eden, that is, from the center of post-anthropoid evolution, the ancestral horde of savage pro-hominids were turned out on the plains to devastate the world.

At last the "perfect" face

As yet there is an immense hiatus in the palæontological history of man, covering at least several million years in the Pliocene epoch. All known

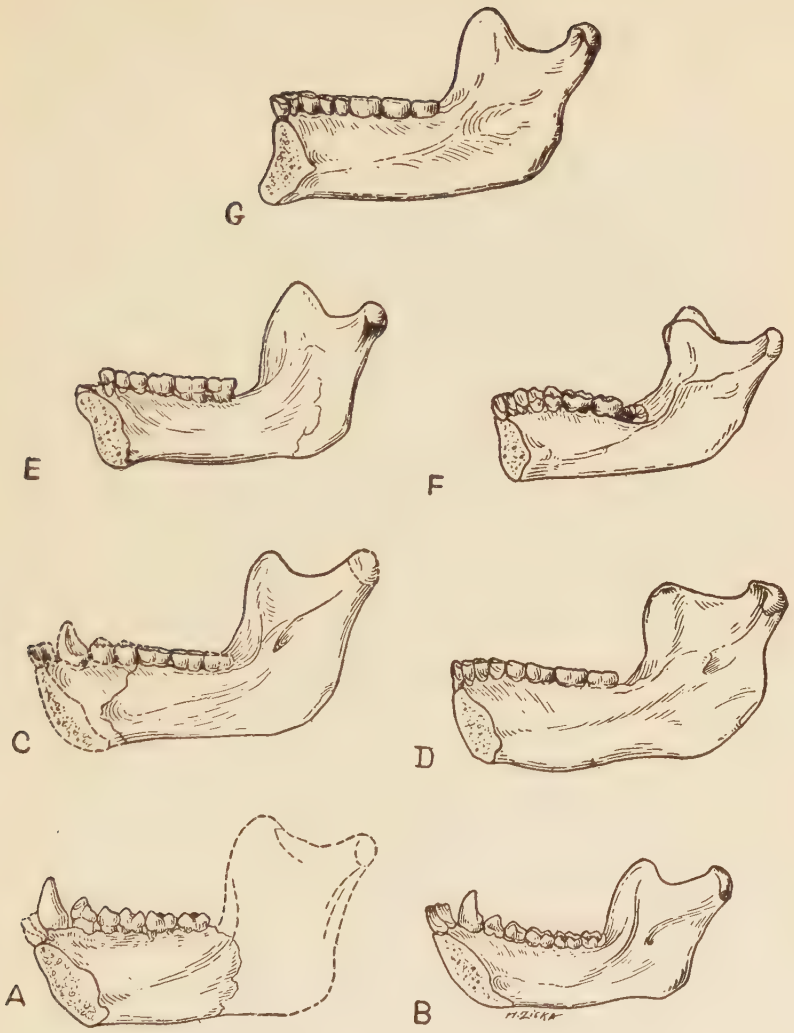

FIG. 45. COMPARATIVE VIEWS OF SECTIONED LOWER JAWS.

A. *Dryopithecus* (after Gregory and Hellman); B. Chimpanzee; C. Piltdown (after A. S. Woodward); D. Heidelberg (after Schoetensack); E. Ehringsdorf (after Virchow); F. Neanderthal (after Weinert); G. Cro-Magnon (after Verneau).

early human fossils are unquestionably human in one way or another—even including the famous *Pithecanthropus*, which zealous anti-evolutionists stoutly refuse to admit to the human family. But it is also noteworthy that each of these earliest human relics is ape-like in a different way. The Piltdown lower jaw (Fig. 41) and teeth are extraordinarily ape-like; the *Pithecanthropus* skull (Fig. 42C) is ape-like both in its projecting brow ridges and in certain features of the occiput, while the braincast, according to all expert analysis, is far inferior in certain respects to that of *Homo sapiens;* the Heidelberg jaw (Fig. 45D) has a receding chin and the Mousterian skull has many primitive ape-like details in the teeth (Fig. 45F) that are usually lost in *Homo sapiens.* The Rhodesian skull (Fig. 42F) shows remarkably gorilla-like details of the bony lower border of the nose, indicating a very low form of nasal cartilages and nostrils; the Talgai (Australia) skull is a proto-Australoid type with extreme prognathism (Fig. 42E). The *Australopithecus* skull (Fig. 42A) is that of a young anthropoid with an exceptionally well developed brain (Dart, Sollas, Broom). While it may be nearer to the chimpanzee than to man, its brain, skull

Fig. 16. The "Almost Human" Skull of Australopithecus, a Young Fossil Anthropoid (after Dart).

Fig. 47. Restoration of the Head of the Young Australopithecus.

(After a drawing by Forrestier made under the direction of Elliot Smith.)

and teeth tend to bridge the gap between the highest apes and the lowest men.

Such were the last fleeting souvenirs of the prehuman stage, surviving millions of years after the first separation of the human and great ape families. They represent various degrees of approximation toward the modernized type of face, from the almost ape-like lower jaw of Piltdown to the highbred old man of Cro-Magnon (Fig. 42G). Thus the scant evidence suggests that even in Lower Pleistocene times there were already several different types of mankind, some (such as Piltdown) more progressive or less ape-like in the shape of the forehead, while more conservative in the form of the dentition and jaw, others (*Pithecanthropus*) with a lower form of forehead and not improbably a more progressive form of jaw. Whether these represent individual, racial or specific difference is not fully demonstrated; in any case they suggest that within the family of mankind there was a remarkably wide range of variability in facial characters, as there still is.

The profound agreement between mankind and the anthropoid group in anatomical characteristics and in physiological reactions and to a certain

extent in basic mental traits (Yerkes, Koehler) all sufficiently establish the fact that at one time the human and anthropoid groups converged backward to a common source. It is also the plain teaching of comparative anatomy that the modernized white human face with its small mouth, weak jaws, reduced dentition, projecting chin, delicate projecting nose and pale skin, has changed far more from the primitive man-anthropoid starting-point than has the face of a young chimpanzee, with huge mouth, strong teeth, receding chin and flat nose. Professor Osborn holds that the separation of man and apes from the primitive anthropoid stock began as far back as the Lower Oligocene epoch, possibly some thirty-five million years ago, while the present writer is inclined to date this event from the next higher epoch, namely the Lower Miocene, possibly nineteen million years ago.[1]

Whichever date, if either, may eventually prove to be the true one, the fact remains that in its present form the modernized human face is *sui*

[1] These figures are according to the tentative estimates of the geological epochs worked out by Barrell by the "radium emanation" method, based on the rate of disintegration of radioactive ores from different geological horizons.

generis, just as the face of any other species of mammal is unique in its specific attributes. But there are thousands of good scientific reasons for accepting as a fact the evolution of man from lower mammals, there is a convincing chain of known forms in the long series from fish to man; and even in civilized man the human face is most obviously related rather closely to that of the anthropoids; therefore only the most confirmed mystic by preference will insist that the evolution of the human face is a "mystery." It is true that every event of the kind abounds in mystery, since no matter how fully we can describe by what stages it happens, we uncover infinitely ramifying problems whenever we attempt to isolate the causal factors.

Undoubtedly when primitive man left the forests and came out on the plains to live by hunting there was a change in food, a change from a frugivorous to at least a partly carnivorous diet, there was a change of locomotion from erect tree-climbing (brachiation) to bipedal running on the plains; speech arose and the brain grew so large that it grew faster than the face; the period of individual growth and development was greatly extended; all

the system of the ductless glands which has so profound an effect upon growth and development was affected in innumerable ways and differently in different individuals and races. Thus we begin to sense the complexity of the factors influencing the emergence of the typical human face from a primitive anthropoid type.

Whatever the causes may have been, the evidence indicates that, starting with a face not dissimilar to that of an immature female chimpanzee (Fig. 40B), the forehead rapidly became larger, the incisor teeth became less inclined, more vertical and smaller in size, the canine teeth diminished in size and in such a way that the tip of the lower one finally passed behind the front edge of the upper canine; the premolars and molars also decreased in fore and aft diameter. In addition to the reduction and backward displacement of the teeth there was a positive outgrowth of the bony chin, which possibly on account of the early development of the tongue could not retreat further backward. The later stages of this process may be reconstructed by comparing the faces of different races, from the projecting muzzles, very large mouth, broad flat nose and retreating chin

of some of the Tasmanians (Fig. 10, Frontispiece) to the narrow, forwardly-projecting, pointed nose and pointed chin of the Alpine, European type (Fig. 11 Frontispiece).

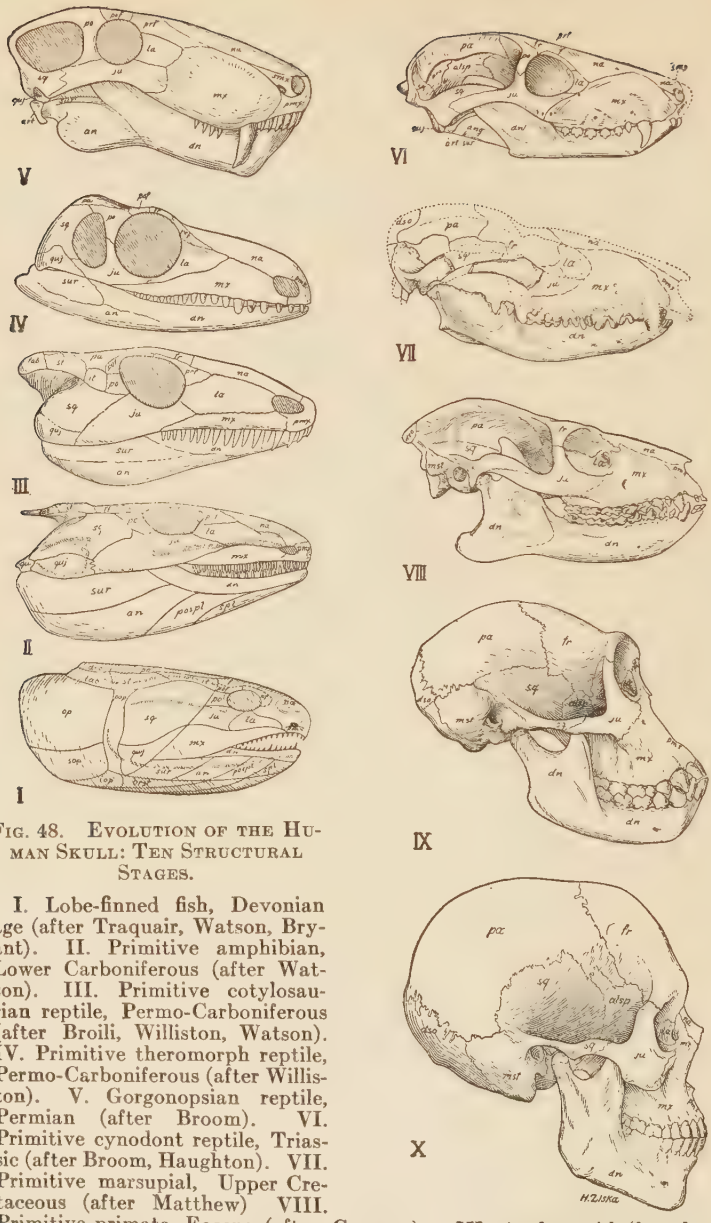

FIG. 48. EVOLUTION OF THE HUMAN SKULL: TEN STRUCTURAL STAGES.

I. Lobe-finned fish, Devonian age (after Traquair, Watson, Bryant). II. Primitive amphibian, Lower Carboniferous (after Watson). III. Primitive cotylosaurian reptile, Permo-Carboniferous (after Broili, Williston, Watson). IV. Primitive theromorph reptile, Permo-Carboniferous (after Williston). V. Gorgonopsian reptile, Permian (after Broom). VI. Primitive cynodont reptile, Triassic (after Broom, Haughton). VII. Primitive marsupial, Upper Cretaceous (after Matthew) VIII. Primitive primate, Eocene (after Gregory). IX. Anthropoid (female chimpanzee), Recent. X. Man, Recent.

For details, see pp. xxii, xxiii.

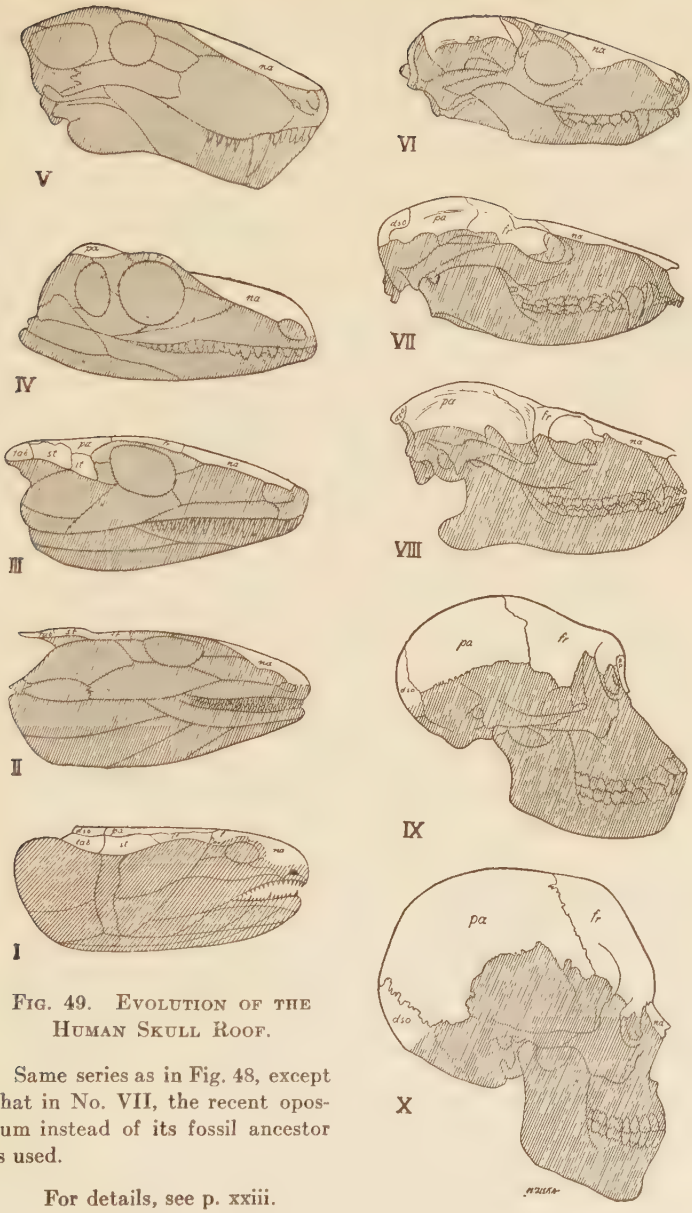

FIG. 49. EVOLUTION OF THE HUMAN SKULL ROOF.

Same series as in Fig. 48, except that in No. VII, the recent opossum instead of its fossil ancestor is used.

For details, see p. xxiii.

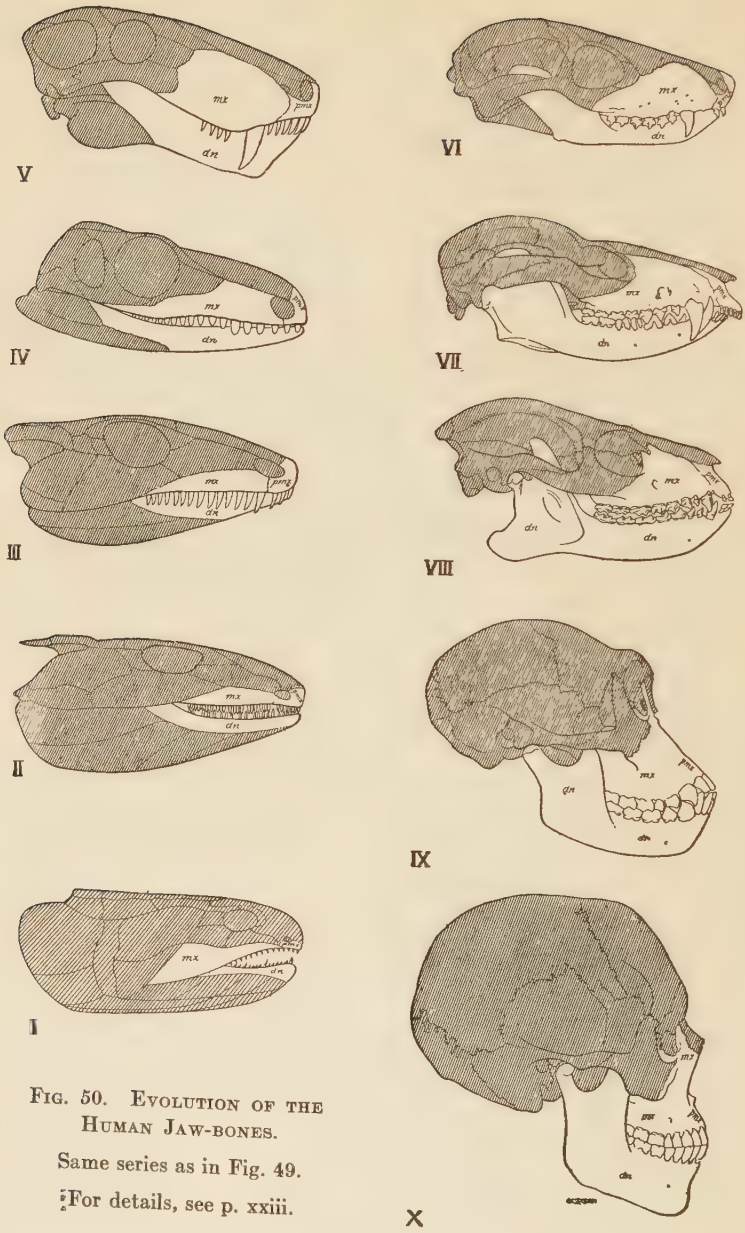

FIG. 50. EVOLUTION OF THE HUMAN JAW-BONES.

Same series as in Fig. 49.

For details, see p. xxiii.

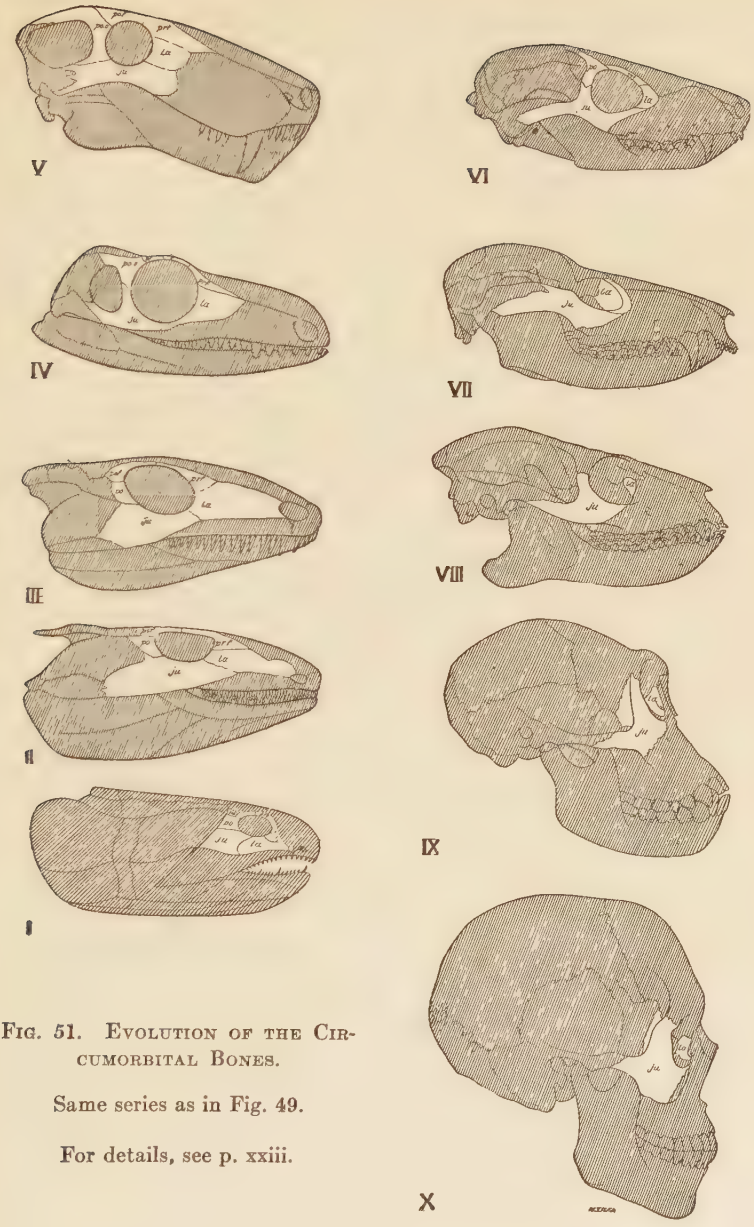

Fig. 51. Evolution of the Circumorbital Bones.

Same series as in Fig. 49.

For details, see p. xxiii.

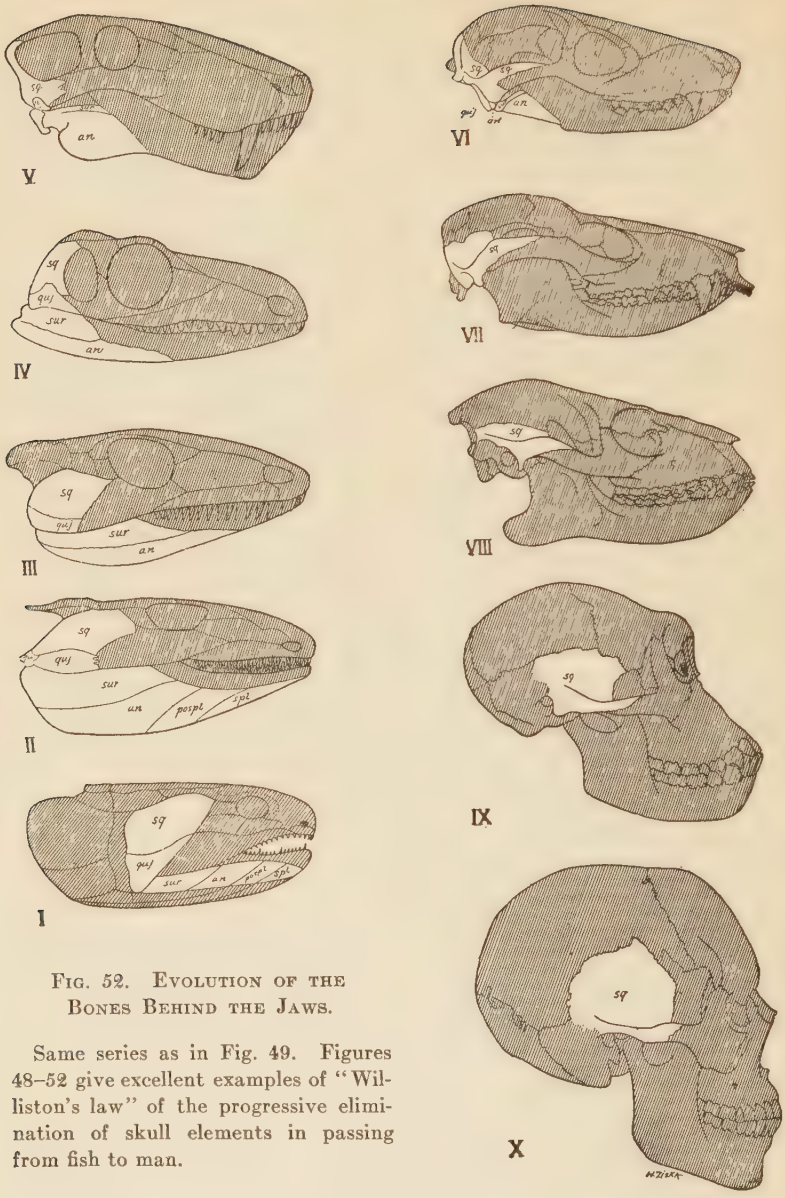

FIG. 52. EVOLUTION OF THE BONES BEHIND THE JAWS.

Same series as in Fig. 49. Figures 48–52 give excellent examples of "Williston's law" of the progressive elimination of skull elements in passing from fish to man.

For details, see pp. xxiii, xxiv.

PART II

CONCISE HISTORY OF OUR BEST FEATURES

The Bony Framework of the God-Like Mask

To review at this point the history of the bony framework of the face, we note that the human skull as a whole is a complex consisting of a chondrocranium, or inner skull, which is preformed in cartilage, and an outer shell of dermal bones, formed in membrane. The chondrocranium comprises the base of the skull, the sphenoid bone and the olfactory and otic capsules. The outer, or dermocranium, comprises: (a) the roofing bones (nasals, frontals, parietals, and the membranous part of the supraoccipital); (b) the orbital elements (lacrymal, jugal, or malar); (c) the squamous part of the temporal bone; (e) the maxillary elements (upper and lower jaw bones); (f) the palatal bone and the internal pterygoid plate of the sphenoid; (g) the vomer.

The illustrations submitted herewith (Figs.

48–53) set forth a few of the facts which have convinced modern anatomists that man, like other mammals, was not created at one stroke, but that he reached his present condition by gradual stages of modification, which, thanks to the unremitting labors of many palæontologists and anatomists, now appear to be fairly well understood. None of these stages is hypothetical; they are either known fossil forms or are the surviving and little-modified descendants of known fossil forms.

From the imperfect nature of the fossil record we can never expect to recover the infinite number of links in the direct line of ancestry of man or of any other mammal. The record affords us only successive structural stages that are more or less nearly related to the main line of ascent from fish to man.

The story told in these illustrations has not been invented by the writer. It has slowly revealed itself as the palæontologists and anatomists of a century past have gradually unearthed it. During the past fifteen years great progress has been made all along the line of stages I to X, either in the discovery of hitherto unknown or little-known forms, or in the determination of the sutural

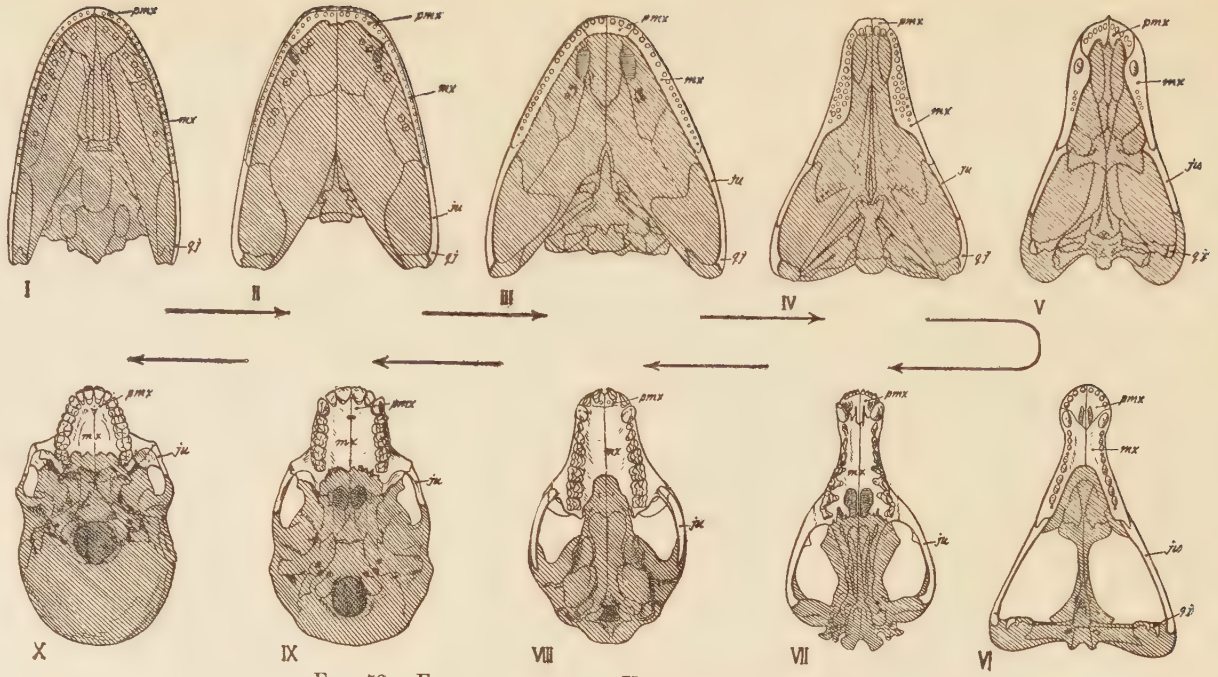

FIG. 53. EVOLUTION OF THE UNDERSIDE OF THE SKULL.

I. Lobe-finned fish, Devonian (after Bryant, Watson). II. Primitive amphibian, Carboniferous (after Watson). III. Primitive cotylosaurian reptile, Permo-Carboniferous (after Watson). IV. Advanced cotylosaurian reptile, Permo-Carboniferous (original). V. Gorgonopsian reptile, Permian (after Watson). VI. Advanced mammal-like reptile, Triassic (mainly after Watson). VII. Marsupial mammal, Recent (original). VIII. Eocene lemuroid primate (after Stehlin). IX. Anthropoid (female chimpanzee) (original). X. Man (Australian aboriginal).

For details, see p. xxiv.

limits of the individual bones, or in the vital problems of determining the systematic relationships of each of the forms figured and of the groups that they represent. Recent palæontologists who have contributed especially to these subjects include D. M. S. Watson (in connection with Stages I, II, III, V, VI), Bryant (in connection with Stage I), Williston (in connection with Stages III, IV), Broili (in connection with Stage III), Broom (in connection with Stages V, VI), Haughton (in connection with Stage VI), Matthew (in connection with Stage VII), Gregory (in connection with Stages VIII, IX). The drawings, like most of the others in this book, were skilfully executed by Mrs. Helen Ziska, working under the constant advice and supervision of the author. For whatever errors the figures may still bear, after many appeals to the original data, the writer alone therefore must be held responsible.

To recapitulate, the outstanding changes in the lateral view of the skull from fish to man appear to have been as follows:

Of the bones on the roof of the skull (Fig. 49), namely the nasals, frontals, parietals, interparietals (or dermo-supraoccipitals) and tabulars, only the

last disappear entirely in the mammals. As the brain enlarges these roofing bones are lifted into greater prominence, the frontals, parietals, interparietals and occipitals becoming the dominant elements in the great vault of the human skull.

The superior maxillary bone (Fig. 50) begins as a slender, vertically shallow element, but by the time of the early mammal-like reptiles (Fig. 50 V) it has extended dorsally and gained contact with the nasals. In the mammals (Fig. 50 VII–X) its dominance is still more pronounced; one fork reaches the frontals while another fork finally separates the lacrymal from the jugal and the whole bone becomes shortened antero-horizontally and deepened vertically. In the anthropoids and man the premaxillæ early unite with the maxillæ.

The inferior maxillary (dentary) at first is confined to the anterior half of the mandible. In the higher mammal-like reptiles it becomes dominant, the post-dentary elements retreating before it. In the earliest mammals the ascending ramus of the dentary effects a new contact with the squamosal, the temporo-mandibular articulation, which is transmitted without further essential modification to man.

Of the bones around the eye (Fig. 51), originally five in number, three (the prefrontal, postfrontal, postorbital) are eliminated by the time of the earliest mammals, so that man inherits only two of the original five, namely the lacrymal and the jugal or malar.

The temporo-mandibular series (Fig. 52), originally including eight bones (the intertemporal, supratemporal, squamosal, quadrato-jugal, surangular, angular postsplenial, splenial), suffers gradual reduction, until in the earliest mammals, as in man, only the squamosal remains, at least in the lateral view of the skull. In the mammals the squamosal has fused with the enlarged periotic mass and in the anthropoids and man the tympanic is added, the whole complex forming the temporal bone.

At every successive stage of evolution advances in skull structure were dependent upon improvements in the brain itself, upon shiftings and enlargements of the parts containing the sense organs, upon modifications of the jaws and teeth, accompanying or accompanied by changes of habits. The skull in turn is closely integrated with both the active and the passive elements of

the locomotor apparatus, a topic which will be developed elsewhere.

To each of the stages described above man owes certain "basic patents," or adaptive improvements which have been of critical importance in his survival. Thus to certain far-off Devonian air-breathing fishes man owes the general ground-plan of the vertebrate skull, the combination of primary "gill-arch" jaws with sheathing or outer jaws, and each and every one of the twenty-eight normal skull bones which he still retains.

Next, he is indebted to the first amphibians for partially solving the innumerable problems caused by emergence from the water. These old pioneers cast off the whole series of bones that covered the branchial chamber and made for themselves an ear-drum out of the skin around the notch where the opercular was formerly located. The early reptiles safeguarded most of the inheritance from their semi-aquatic ancestors, dropping only the inter- and supratemporals. To the first of the mammal-like series man owes the beginnings of his temporal fossa and zygomatic arch, and the dominance of the superior maxilla. From the higher mammal-like reptiles he has inherited the

further development of the temporal fossa and especially the dominance of the inferior maxillary or dentary bone of the lower jaw. To these progressive pro-mammals man can render thanks for the differentiation of his dentition into incisors, canines, premolars and molars, and apparently he can also thank them for the reduction of the numerous successional teeth to two sets, corresponding to the milk teeth and the permanent set.

The earliest mammals invented one of the most useful features of man's skull by eliminating from the masticatory apparatus all the elements lying behind the dentary and by establishing the temporo-mandibular joint. They also cast off the reptilian prefrontal, postfrontal and postorbital bones and cleared the way for the final simplification of the bony scaffolding of the face.

To the earliest primates, well schooled in arboreal life, man owes the first steps in the glorification of the eyes, which become increasingly dominant. These still lowly but thrifty forebears made good the loss of the reptilian postorbital bar by elaborating a new one from conjoining processes from the frontal and jugal (or malar) bones.

But still greater was our debt to the arboreal

pro-anthropoids, those intelligent beings who elected to develop sight at the expense of smell. These skilled acrobats, moving in a vertical position, met and solved a new series of problems connected with the turning downward of the skull upon the upright column. They also made the first notable attempts to shorten and deepen the face and even took a long step toward enlarging the brain and brain chamber.

Starting with these and many like advantages gained during a long training in arboreal life, it was the task of our relatively nearer precursors (beginning possibly in Miocene times, or earlier) to re-adapt all these arboreal adaptations for a life on the ground and to take the final steps upward that have brought humanity to its present levels of intelligence.

Wholly ignorant of the facts, the ancient Jewish priests indulged themselves in the fancy that man was made in the image of God; but modern science shows that the god-like mask which is the human face is made out of the same elements as in the gorilla; and that in both ape and man the bony framework of the face is composed of strictly homologous elements, inherited from a long line of lower vertebrates.

Fish-Traps and Faces

THE FIRST MOUTHS

From air-breathing fish to man the *general* course of evolution seems clear enough, at least in its broad outlines. But when we inquire whence

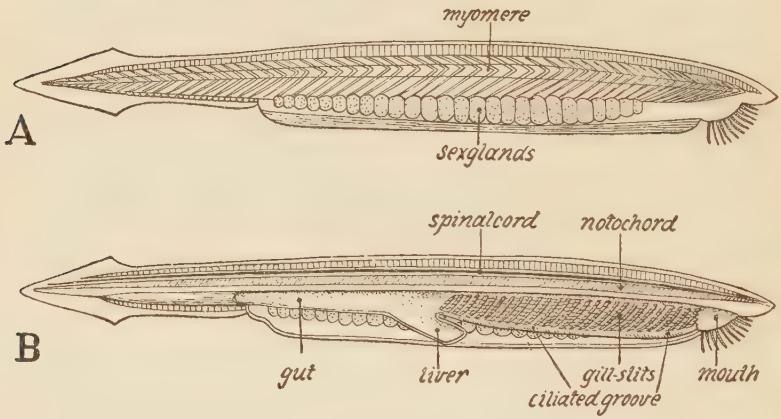

Fig. 54. Anatomy of the Lancelet, the Most Primitive Living Chordate Animal (after Delage and Hérouard).

A. Entire animal, seen as a semi-transparent object; B. Longitudinal section. For details, see p. xxiv.

came the fish, the evidence while extensive is somewhat ambiguous and there is room for sharp differences of opinion. On the one hand, there is Professor Patten, who derives the whole vertebrate series from very ancient jointed animals remotely allied to the modern scorpions and *Limulus;* on the other hand, there are the more orthodox

zoologists, who infer that the greatly simplified form *Amphioxus* (Fig. 54), together with all the vertebrates, represent offshoots of some still undiscovered stock that also gave rise to the acorn-worms (*Balanoglossus*), the starfishes and certain other peculiar groups. According to this view,

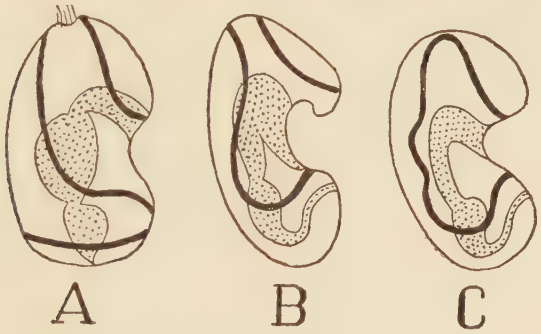

Fig. 55. Larvæ of Echinoderms: Sea-cucumber (A), Starfish (B) and of the "Acorn-worm" (after Delage and Hérouard).

For details, see p. xxv.

the common ancestors of all these diversified groups were exceedingly simplified, free-swimming, marine organisms, consisting chiefly of a digestive tube bent at a right angle and enclosed in a thin balloon-like tissue, more or less folded into plaits and provided with strips of cilia, by the lashing of which the floating bag moved slowly through the water. Such forms (Fig. 55) are found living today as the larvæ or young stages of starfishes,

sea-cucumbers, and also of the acorn-worm *Balanoglossus*. The mouth of these forms is the original mouth of the primitive gut or digestive tract.

There is evidence from embryology that the mouth of the vertebrates is a compound structure

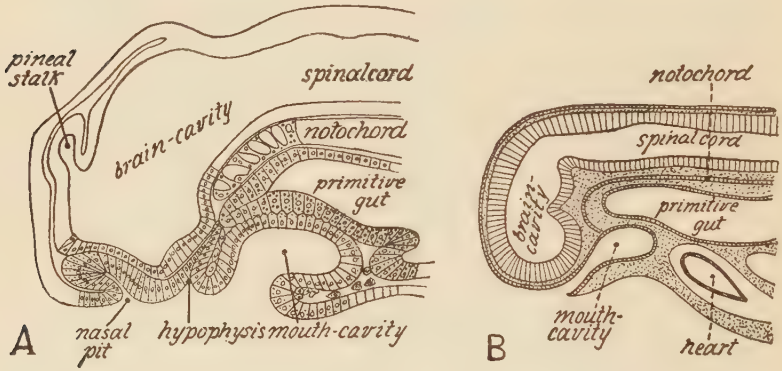

Fig. 56. Inner and Outer Mouth Pouches in Embryo Vertebrates: Larval Lamprey (A) (after Minot); Embryo Rabbit (B) (after Mihalcovics).

For details, see p. xxv.

formed from the union of a down-pocketing of the outer layer or ectoderm, meeting a pouch growing out from the primitive gut. These inner and outer mouth pouches in the early embryos of lampreys, sharks and higher vertebrates, are similar to the inner and outer pouches that give rise to the gill openings, with which indeed they are supposed to be homologous. Moreover Stensiö has recently shown that in the cephalaspid

ostracoderms (Fig. 57) the mouth cavity was in series with the cavities of the gill openings and was probably homologous with them.

The predecessors of the vertebrates probably fed upon small organisms and organic matter,

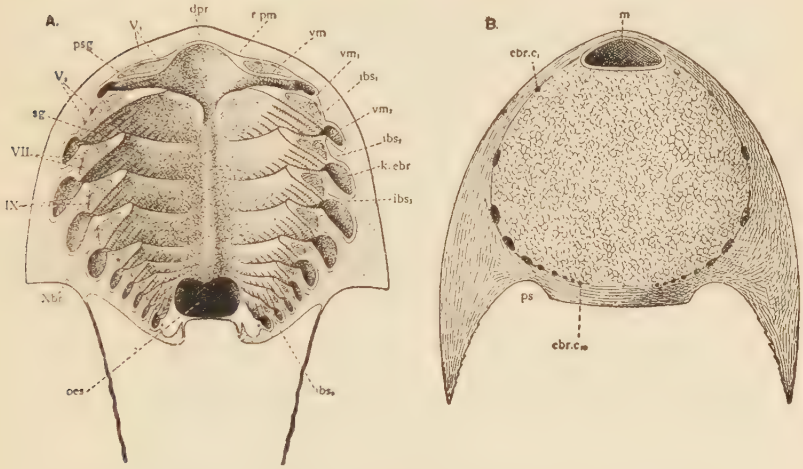

Fig. 57. Attempted Restorations of the Mouth and Gill Region of Two Cephalaspid Ostracoderms by Stensiö.

For details, see p. xxv.

which were scooped into the mouth cavity and may have been passed along to the stomach by the lashing of cilia located in a groove, as in the living *Amphioxus* (Fig. 54).

This method of ingestion by means of cilia may also have been practised by some of the ostracoderms, the earliest known forerunners of the

vertebrates (Figs. 4, 57). Such food habits would seem reasonable both for those ostracoderms, like *Pteraspis* (Fig. 4D), which had narrow mouths placed below a long rostrum and therefore adapted for feeding in the mud, and for those like *Trematapis* (Fig. 4B, C) in which the fore part of the body was flattened into a broad rounded shovel and the mouth was a wide slit-like opening at the

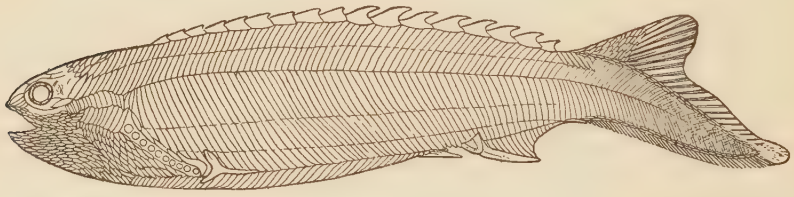

Fig. 58. Swift-moving Ostracoderm from the Silurian of Norway (after Kiaer).

For details, see p. xxv.

front border of the head. In *Cephalaspis* (Fig. 57B) also the mouth appears to have been in series with the gill-arches.

But there were still other ostracoderms of the order Anaspida (Fig. 4A), in which the body-form seems adapted for swift movement through the water and in which the mouth, while not too large to be powerful, was strengthened by a bony strip with a knob on its front end. Such ostracoderms may have already embarked on the career of

piracy which seems to have characterized the more remote ancestors of man for countless ages. But up to this point in their evolution true teeth had not been attained by the early predecessors of the vertebrates.

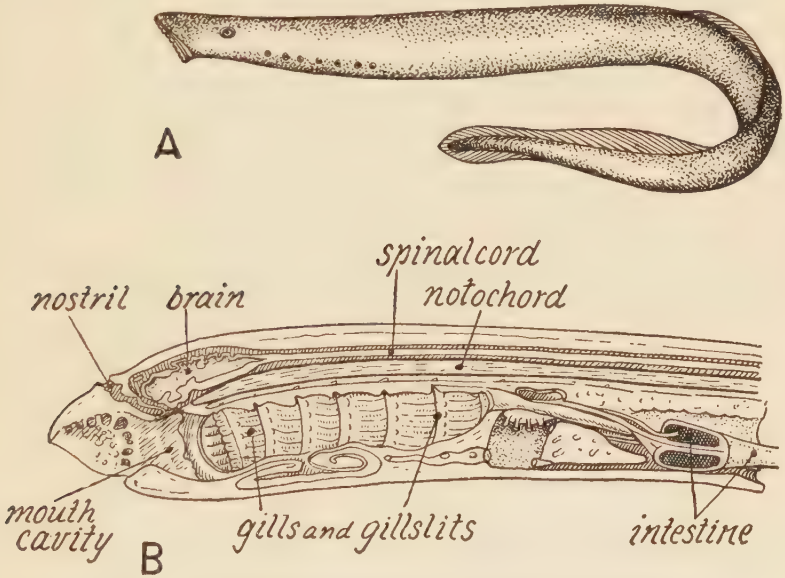

FIG. 59. A MODERN DESCENDANT OF THE OSTRACODERMS.

A. Adult lamprey (after Jordan and Evermann); B. Longitudinal section of larval lamprey, enlarged (after Goodrich).

THE BEGINNINGS OF TEETH

The ostracoderms as a whole may be transitional between the method of "ciliary ingestion" and the devouring of living flesh by the existing cyclostomes (lampreys, hags), which Stensiö has

shown to be the highly specialized, eel-like, and in some respects degenerate derivatives of the ostracoderms of Silurian times. Even today (Fig. 59) in the early larval lamprey (*Ammocoetes* stage) the pharynx is provided with a prominent "ciliated groove," which (like that of *Amphioxus*) appears to be reminiscent of the earlier days of feeding on microscopic organisms; the adult lamprey, on the other hand, is a cruel pirate, rasping off chunks of flesh from the sides of helpless fishes and occasionally eating its way, it is said, into their interiors, finally reducing them to floating shells.

The lampreys and their allies are enabled to carry on their nefarious business by means of thorny teeth, set in concentric rows about the mouth and flanking a protrusile rasp, which is likewise covered with horny teeth and can be drawn back and forth like the rasp of a whelk.

The teeth of the lampreys (Fig. 60A) are of extraordinary interest, since they have always been regarded as representing a very early stage in the evolution of the teeth of vertebrates. Each tooth consists of a thick, horny, epithelial thorn with a pulp cavity within, which is ready to grow another thorn as soon as the outer one is broken

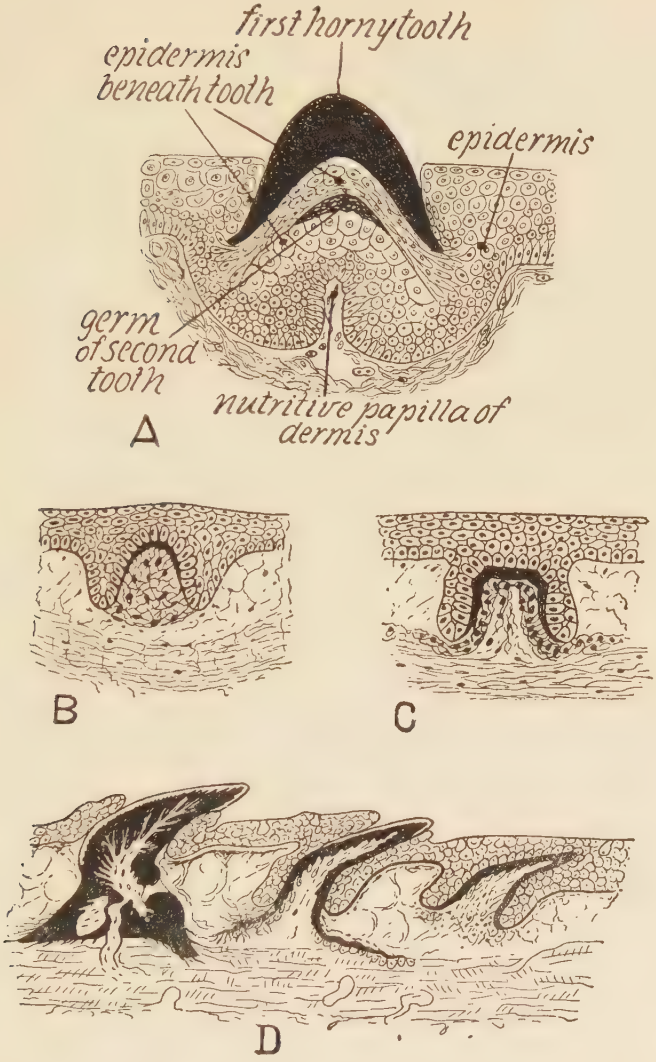

FIG. 60. DEVELOPMENT OF TEETH IN LAMPREY (A) AND SHARK (B, C, D). (AFTER GOODRICH.)

For details, see p. xxvi.

off or shed. Nevertheless the teeth of the higher vertebrates probably arose not from horny epithelial teeth like those of the modern lampreys, but from enamel-covered shagreen denticles such as covered the whole body of *Lanarkia*, one of the Scotch Silurian ostracoderms. In the sharks (Fig. 60B, C, D) each little shagreen denticle on the surface of the skin consists of a little cone in which a porcelain-like layer of "enamel" is laid down between the epithelial covering and the pulp cavity. These shagreen denticles, together with the stratified bony deposits in the deepest layers of skin, gave rise not only to the teeth of higher vertebrates but also to the enamel-covered bony plates that cover the braincase, the bony tooth-bearing plates that cover the primary cartilaginous jaws and the bony tooth-bearing plates on the roof of the mouth, both in the air-breathing, lobe-finned fishes and in their successors, the earliest amphibians.

These enamel-covered plates were also homologous with the bony ganoid scales on the surface of the body.

Thus we are again reminded of the remarkable potentialities of the many-layered skin in the

ancestors of the vertebrates, since it gave rise in different groups to horny thorns, to shagreen denticles, to true stratified bony scales, to enamel-covered skull plates, as well as to many different kinds of sense organs.

Nor can it be too often pointed out that the whole organization of primitive vertebrates was adapted for the pursuit and capture of living prey, that sharp teeth were made from the shagreen of the skin, first for holding and then for cutting living prey, that in every geological age until we reach the primitive anthropoid stock of relatively recent times, the herbivorous forms, derived from the more primitive carnivores, acquired various types of specialized teeth which could never have given rise to the higher carnivorous types. Any hypothesis that would derive the earlier carnivorous vertebrates from herbivorous predecessors would be definitely contradicted by all the available evidence afforded by a comparative study of the brain, sense organs, the locomotor apparatus and the digestive system.

After a century of intensive research we can only speculate, almost idly, as to what may have been the mode of origin of the mouth, jaws and

teeth below the ostracoderm grade of evolution. But when we reach the grade of evolution represented by the shark, we find that *the shark stands unquestionably nearer to man in the construction of its jaws and teeth than it does to any known group of invertebrates; while between shark and man many intermediate conditions of the mouth are definitely known.*

THE PRIMARY JAWS

The gill pouches of fishes and of the embryos of higher vertebrates, including man, are supported by cartilaginous bars (Figs. 7, 8), the so-called "visceral arches," and the mouth pouches of sharks and embryo vertebrates are likewise supported by cartilaginous bars, the oral cartilages, which have every appearance of belonging in series with the gill arches. The primary upper jaw cartilages, one on either side, are called the palatoquadrate cartilages, while the primary lower jaw cartilages are called Meckel's cartilages, or the mandible. The "labial cartilages" in front of the jaws (Figs. 7, 8) are possible remnants of at least one "premandibular" arch.

In the predecessors of the sharks, we may infer,

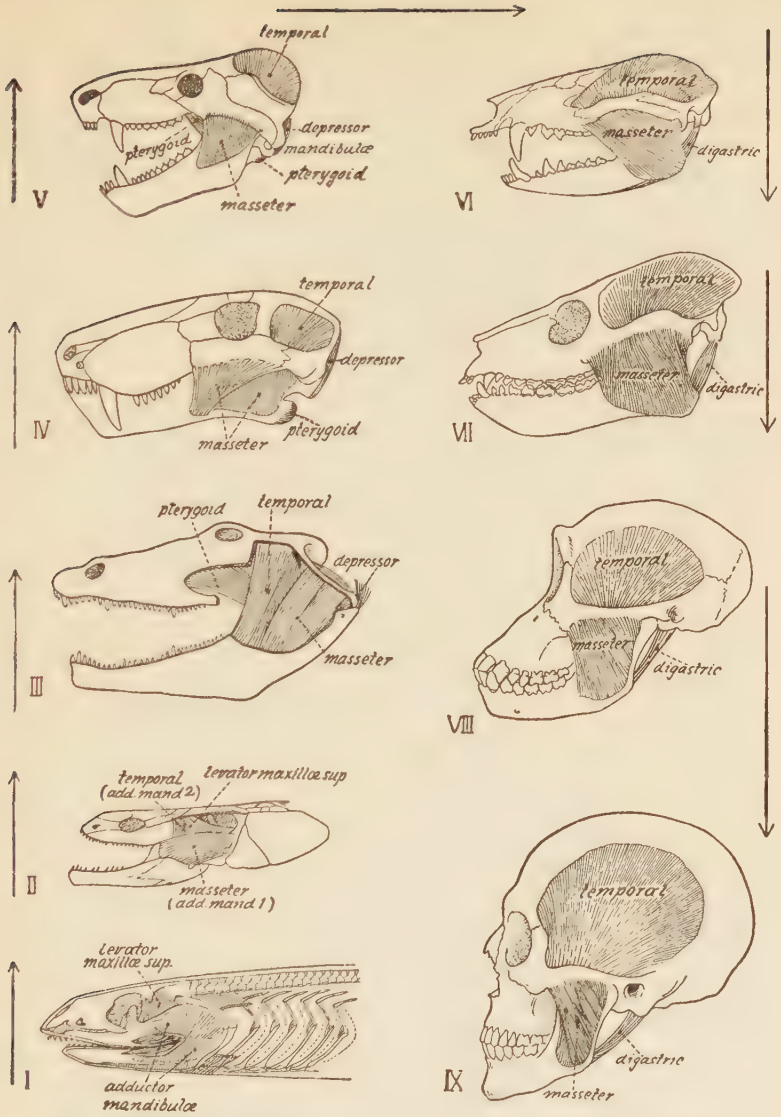

FIG. 61. EVOLUTION OF THE JAW MUSCLES FROM FISH TO MAN.

I. Shark (data from Allis). II. Lobe-finned ganoid (after L. A. Adams). III. Primitive amphibian (after L. A. Adams). Restoration. IV. Primitive mammal-like reptile (skull mainly from Broom). Restoration. V. Advanced mammal-like reptile (after L. A. Adams). Restoration. VI. Primitive marsupial (after L. A. Adams). VII. Primitive primate. VIII. Chimpanzee. IX. Modern man.

For details, see p. xxvi.

none of these "visceral arches" (labial cartilages, jaws or gill arches) were connected with the brain-case except by connective tissue and as the living prey was presumably small there was no need of special bracing for these arches. But as the race grew larger the size of the prey likewise increased and convulsive swallowing efforts were made by the fish to force the prey past the region of the gill pouches down into the stomach. At the same time the contractile muscles around the whole branchial series grew stronger, those attached to the future jaw arches increased faster than their fellows and so did the future jaws themselves. In this way the jaw muscles of the shark and of higher vertebrates (Fig. 61) were apparently derived by enlargement from muscles corresponding to the constrictor muscles of the gill arches.

For a long time the primary upper jaw was suspended from the skull mainly through its attachment to the second or hyoid arch (Fig. 62A) but in the amphibians and higher vertebrates the primary upper jaw itself becomes attached to the skull (Fig. 62, B, C). When large tooth-bearing bony plates came to sheath and cover over the primary upper and lower jaws they gradually

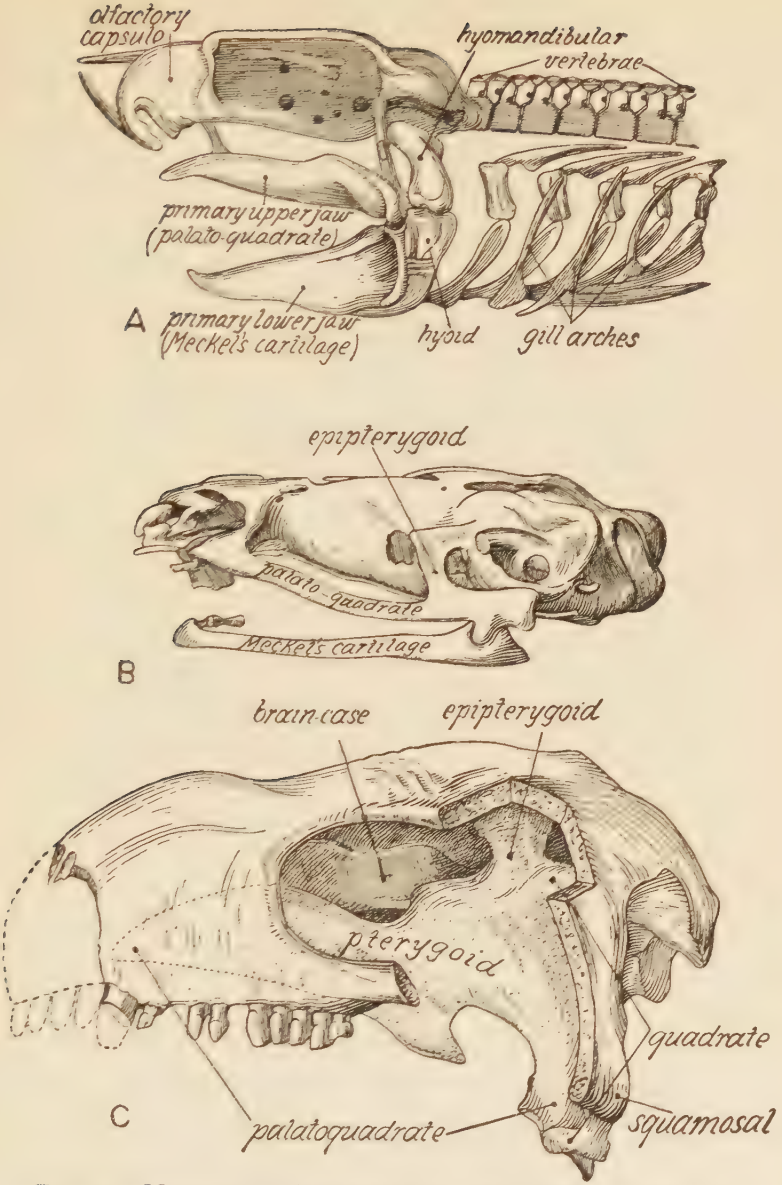

FIG. 62. METHODS OF ATTACHMENT OF THE PRIMARY UPPER JAW TO THE UNDER SIDE OF THE SKULL.

In C the bony mask covering the temporal region is cut through and a part of it removed to show the primary upper jaw and its relations to the braincase. For details, see pp. xxvi, xxvii.

supplanted them, at least in the tooth-bearing regions. In mammals (including man) clear traces of the primary upper jaw may be found in early embryonic stages of development (see Keith, *Human Embryology and Morphology*, 1921, pages 138, 148, 172).

THE RISE OF THE SECONDARY JAWS AND THEIR TEETH

Up to the present time we have been dealing with the origin and early evolution of the *primary* upper and lower jaws, but in the higher vertebrates, including man, these primary jaws are completely overshadowed and masked by the *secondary* jaws. In the sharks the secondary jaws are represented merely by the skin that is wrapped around the primary jaws, or palatoquadrate and Meckel's cartilage, both on the outside and on the inside of the mouth. In the sharks this skin has no bony base but in the higher fishes and early amphibians the primary upper and lower jaws are covered with many-layered bony plates originally provided with a porcelain-like surface of "ganoine" and usually bearing numerous teeth. In the early lobe-finned, air-breathing fishes (Figs. 11, 12)

these plates are of exactly the same nature as the roof-bones of the skull and the scales on the body. Thus arises the hard "facial mask" so often referred to in the preceding pages.

As used in this book the term "secondary jaws" is limited to the tooth-bearing plates covering the external borders of the primary upper and lower jaws. There are three of these elements on each side of the head throughout the series (Fig. 50) from fish to man and their amazing constancy is an item of evidence of the unity of plan and origin of all the higher vertebrates. The first of these secondary jaw elements is the *premaxilla*, one on each side of the mid-line, at the front end of the jaw; this is followed by the *maxilla*, one on each side behind the premaxillæ. When we compare the under side of the skull (Fig. 63, I, II) of one of the fossil lobe-finned (crossopt) ganoids of the Devonian with that of one of the early amphibians of the Coal Measures, we can hardly doubt that the premaxilla and maxilla of the former are each completely homologous with the corresponding element in the latter. And from the earliest amphibian to man they can be traced in convincing detail (Figs. 50, 53).

The third of the secondary jaw elements is the *dentary* bone, one on each side of the lower jaw. In the lobe-finned or crossopt fishes this bone,

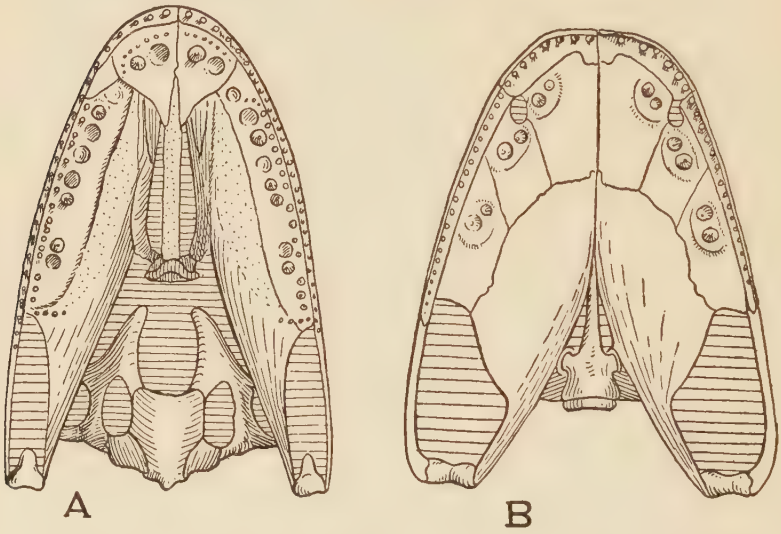

FIG. 63. UNDER SIDE OF THE SKULL OF DEVONIAN FOSSIL FISH (A) AND PRIMITIVE FOSSIL AMPHIBIAN (B). (A AFTER BRYANT AND WATSON; B AFTER WATSON).

The secondary upper jaws are on the margins; the primary upper jaws are largely covered by tooth-bearing plates of the primary palate.

For details, see p. xxvii.

while bearing a stout series of teeth, had not yet assumed the primacy it acquired in later types. We have already (pages 36–39) traced its progress in the mammal-like reptiles and have seen it encroach on the other membrane bones of the lower jaw until it finally secured a contact with the

squamosal bone covering the side of the temporal part of the skull, by which time it had succeeded in crowding its fellows quite off the map.

Meanwhile, how did the crossopts and early amphibians acquire the strong teeth with which they carried on their predatory lives? In the most primitive sharks (Fig. 5) the shagreen-bearing skin is rolled around over the upper and lower jaw cartilages and as the old teeth are broken off the new teeth are gradually pushed up into place on the edge of the jaws in a continuous succession. In the typical sharks the tooth-bearing roll of skin lies in a depression in the calcified cartilaginous primary upper and lower jaws, but the teeth are not separately connected with the jaws and when in use are tied in place only by the strong dental ligament attached to their bases.

In the crossopts (lobe-finned fishes) of the Devonian period the primary upper jaw (palato-quadrate), now completely saturated with bone cells, is covered with bony dermal tracts bearing teeth, some very large and compressed, some small and conical. In front there is also a pair of tooth-bearing dermal plates, the prevomers, on either side of the mid-line. Likewise the secondary

upper jaws, the premaxilla and maxilla, bear compressed conical teeth. The dentary plate of the lower jaw (Fig. 64) covering the outer side of the primary lower jaw or Meckel's cartilage, bears a row of conical teeth which fit between the marginal teeth of the secondary upper jaw and the larger teeth on the dermal plates covering the primary upper jaw. Thus we have the teeth of the secondary upper jaw over-hanging or biting outside of those of the dentary or lower jaw, an arrangement that persists throughout the subsequent series upward to the primitive mammals, traces of it even being preserved in man. The coronoid bones, covering the inner side of the primary lower jaw, in the lobe-finned fish bear large teeth which doubtless sheared into the struggling prey and pressed it against the large teeth on the roof of the mouth. Thus neither the Meckel's cartilage, or primary lower jaw, nor the palato-quadrate, or primary upper jaw, now have any direct relations with the teeth, which are supported entirely on their own bony plates, as they are in all higher vertebrates, including man. The primary lower jaw from this point onward takes a subordinate part, except that its nearer (proximal)

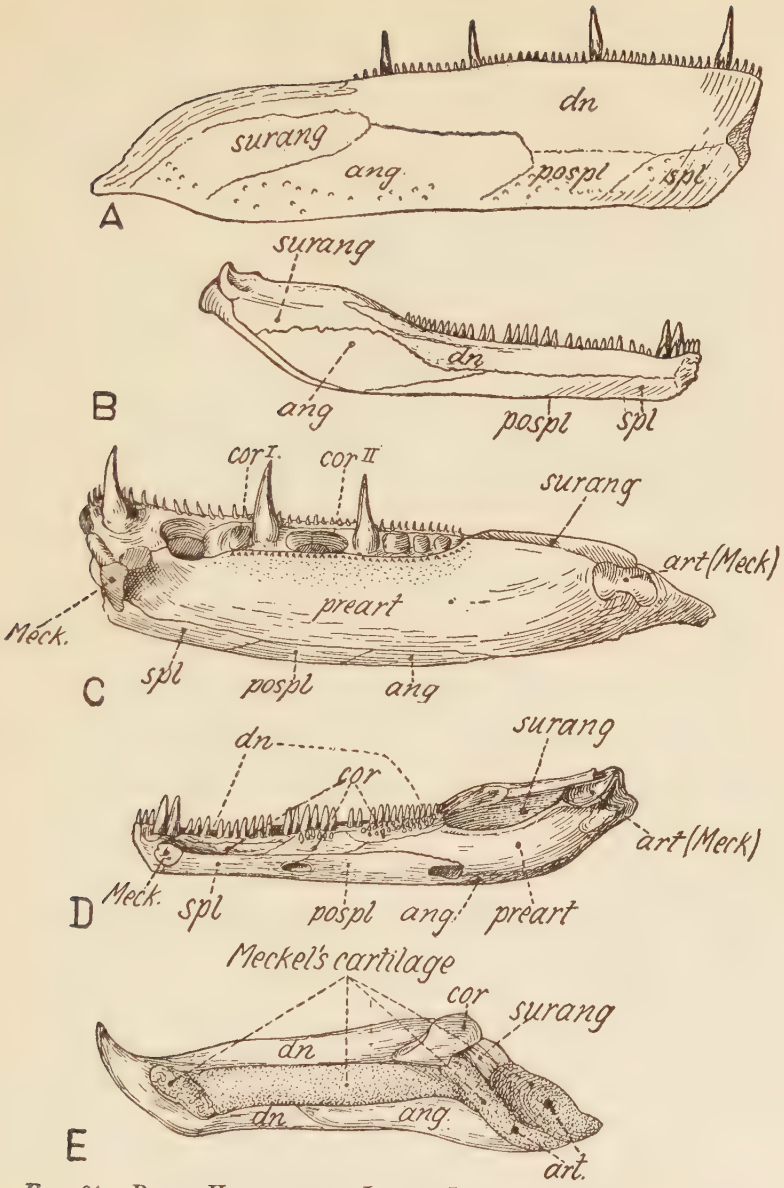

FIG. 64. RIGHT HALF OF THE LOWER JAW OF LOBE-FINNED FISH (A, C) AND PRIMITIVE FOSSIL AMPHIBIAN (B, D), AND RECENT TURTLE EMBRYO (E). (A, C, AFTER WATSON; B, D, AFTER WILLISTON; E, AFTER PARKER.)

For details, see pp. xxvii, xxviii.

end, after becoming ossified (after which it is called the *articular* bone) serves for the main articulation of the lower jaw with the primary upper jaw; this arrangement persists from the crossopt fishes up to the most advanced mammal-like reptiles, which are the immediate predecessors of the mammals.

Each tooth of the above described fossil crossopt fishes consists essentially of an enlarged cone with an open pulp cavity, the sides of the cone being very deeply infolded toward the base, so that in cross-section the primary and secondary folds give rise to the characteristic labyrinthodont pattern (Fig. 18). The surface of the tooth is deeply covered with enamel-like ganoine, which is folded into the primary and secondary folds, and the interior consists of dense, stratified bone or dentine. The derm bone which bears the tooth is strongly attached to it and is folded into its sides along with the primary and secondary folds.

This labyrinthodont mode of attachment of the teeth to the jaw bones is a far more primitive and important method than any of those commonly cited in textbooks on comparative dental anatomy, which usually describe only the either degenerate

or highly specialized modes of attachment found in modern amphibians and reptiles, since it was the starting-point of the conditions found in the higher vertebrates, including man.

To sum up then, the lobe-finned fishes exhibit a great advance upon the sharks toward the amphibians and higher vertebrates in the following respects: (1) the primary upper and lower jaws are now covered with tooth-bearing bony plates, only the back part of the primary upper jaw (forming the quadrate bone) and of the primary lower jaw (forming the articular bone) being exposed and forming the articulation between the upper and lower jaws; (2) the secondary upper and lower jaw (premaxilla, maxilla, dentary) for the first time appear as ossified tooth-bearing plates, which may be compared directly with those of amphibians and higher vertebrates; (3) each tooth represents an enlarged denticle with the base infolded into the labyrinthodont pattern. It is fastened to the bone by the infolding of the latter into the labyrinthodont folds; (4) thus the upper and lower jaws as a whole are of complex construction, including a large number of distinct bony plates, some of which disappear as we pass

to the higher vertebrates, but three of which (premaxilla, maxilla, dentary) persist even in man (Fig. 50).

All these highly predatory adaptations were transmitted by heredity to the oldest known amphibians of the Coal Measures, which are at the very least rather close relatives if not actual descendants of the osteolepid crossopts. The chief advance in these oldest amphibians is the elimination (Fig. 17) of the whole series of plates connected with the opercular tract and consisting of the plates named operculum, suboperculum, interoperculum, preoperculum, and a series of small lateral gulars or branchiostegals. All these were sacrificed when the amphibians eliminated the internal gills in the adult stage.

The loss of these plates not only constitutes a fine example of Williston's law of the progressive reduction in the number of bony elements, as we pass from fish to man, but also serves to bring out the fact that *evolution proceeds fully as much by the loss of superfluous parts as by the further differentiation of those that remain* (Figs. 50, 52).

Many of the amphibians adopted the easy method of lying in wait in the water for their prey,

perhaps even with their mouths open, and then suddenly engulfing it in a living trap. Such a line of specialization leads often to wide flat skulls and very shallow, widely-bowed jaws set with rather small teeth on the margins and a few larger piercing teeth on the roof of the mouth, as in the great labyrinthodonts or stegocephalians of the Permian and Triassic periods. Others, in which the jaws became very long and narrow, actively swam in pursuit of fishes. But those amphibians (*e.g.* Fig. 48 II) which were destined to give rise to the line of ascent to man, avoiding both these extremes, had jaws of only moderate length and a skull of moderate width and considerable depth, especially toward the rear end. At first they retained the teeth on the roof of the mouth (Fig. 53, II–IV) but in the series of reptiles (Fig. 53, V) that finally culminated in the cynodonts (Fig. 53, VI) and probably in the mammals (Fig. 53, VII), the teeth on the roof of the mouth, that is, on the primary upper jaw, were eliminated and the marginal teeth on the secondary jaws acquired the typical dog-toothed or caniniform type of predatory animals that pursue their prey on land.

From this condition there are intermediate stages

to the essentially mammal-like dentition of the cynodonts (Fig. 50 VI), in which the adult dentition, as in man and other mammals, consists of incisors, canines, premolars and molars, and in which the dentition was apparently reduced to two sets corresponding to our milk and permanent teeth. Moreover, each tooth in the cynodonts was set in a distinct socket as in the mammals. Hence these reptiles had already traveled far on the long road from fish to man.

We have followed some of the progressive changes in the jaws of these forms, in which the dentary bone finally became the predominant element and gained contact with the squamosal bone of the skull (Fig. 21), while the bones behind the dentary were reduced to slender proportions (Fig. 52). These changes, however they may have been initiated, were obviously associated with a great development of the temporal, masseter and pterygoid muscles of the jaws (Fig. 61), which have very strongly braced areas of origin and attachment. To the activity of the temporal muscle we apparently owe the first appearance of the temporal fossa (Fig. 48 IV) in the shell of bone that formerly roofed over the jaw muscles, while

to the increase in size of the pterygoid muscles may safely be ascribed the pinching together of the opposite pterygoid bones and the development of a high bony crest on the mid-line of the base of the braincase (Fig. 53 V).

Turning again to the teeth, we may summarize their early history as follows: In some of the Silurian ostracoderms (*Lanarkia*) the teeth of later vertebrates are represented by thorny shagreen denticles embedded in the skin all over the surface of the body, but the ostracoderms themselves did not have teeth in the mouth. In the sharks the skin on the inside of the mouth and jaws carries the teeth, which represent only enlarged dermal denticles. In the sharks the tooth-bearing skin on the inner side of the jaws is rolled inward in a spiral manner and as the old teeth are broken off the new ones unwind or rotate into place.

In the lobe-finned or crossopt fishes, representing the ancestors of the amphibians, at least the larger teeth arise from pockets of bone sunk below the surface of the bony enamel-covered skin. In these forms the bases of the teeth are deeply and complexly infolded and the pockets of bony skin

are infolded into the bases of the teeth. The teeth succeed each other in an oblique series. In *Seymouria*, a fossil reptile from the Permo-Carboniferous of Texas, which is almost on the borderline between the primitive amphibians and all the higher levels of vertebrates, clear traces of the labyrinthodont method of tooth-attachment are still visible, but by the time of the higher mammal-like reptiles all traces of the older method had been lost and the teeth are set in sockets as in the mammals, including man.

ORIGIN OF THE MAMMALIAN PALATE

No less important in determining the course of future evolution in the mammals and in man were the progressive changes in the palatal region (Fig. 53). In the early amphibians the air taken into the olfactory chamber was passed through a pair of tubes opening by the choanæ (Fig. 53 II, *cho.*) or internal nostrils, into the fore part of the roof of the mouth, and from this point the inspired air was practically swallowed, or forced backward by the action of the throat muscles to the opening of the windpipe. In the early mammal-like reptiles (Fig. 53 V) the choanæ opened

into a depression or chamber lying considerably above the general level of the tooth-bearing margins of the upper jaw and they may have been the beginning of a fleshy palate. In the higher mammal-like reptiles or cynodonts (Fig. 52 VI) a secondary palate or bony roof of the mouth was formed by horizontal ledges that grew out from the palatine (*pl*) and maxillary (*mx*) bones and formed a shelf below the chamber where the internal nostrils opened. Very possibly the increasing muscular power and mobility of the tongue, which pressed against the inner side of the upper tooth-bearing bones, may have favored the evolution of bony shelves from the palatine and maxillary bones. In the mammals (Fig. 52 VII–X) (including man) this process is carried much further so that in the adults the bony palate is prolonged much farther backward. To the rear end of this bony palate the soft palate was attached. In this way the naso-pharyngeal air passage was formed, by means of which the inspired air is delivered almost directly to the windpipe, instead of having to pass through the food-containing cavity of the mouth. All this is associated in the higher mammal-like reptiles and

early mammals with the very active respiration of carnivorous animals.

The anti-evolutionists may be interested to learn that at a very early stage of its development the human embryo (Fig. 65) passes through a stage in which the olfactory capsules, like those of sharks, have no internal opening on the palate but are

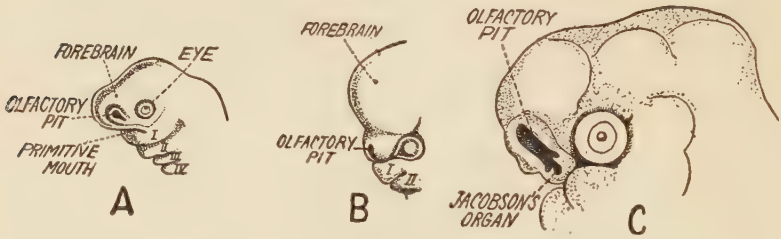

Fig. 65. Early Embryonic Stages in the Development of the Nose in Man (after Keith).

merely extended backward and downward toward the mouth. Later (Fig. 66) the choanæ, or internal openings of the olfactory capsules, develop in the fore part of the roof of the mouth, but there is only the beginning of a secondary palate and the conditions in the reptiles (Fig. 66B) are recalled (Keith, Corning).

In this connection Keith (1921, pp. 158, 159) summarizes the evolution of the human face as follows:

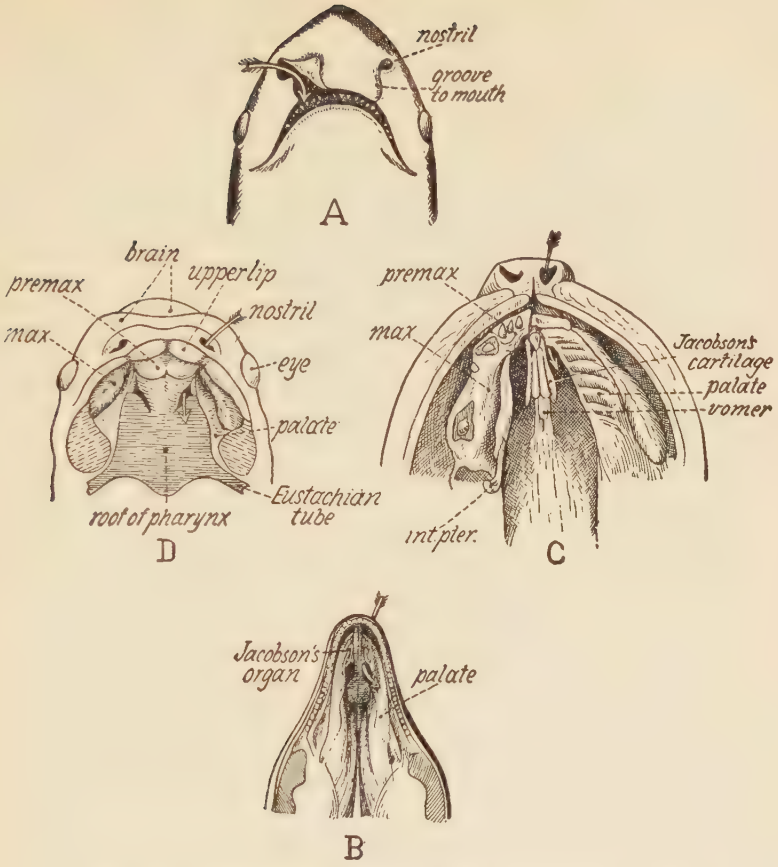

FIG. 66. COMPARATIVE ANATOMY OF THE HUMAN PALATE.

A. Recent shark, showing groove from nose to front of mouth. (After Keith.)

B. Lizard, in which internal opening (choana) from the nose opens in the forepart of the mouth cavity. (After Plate.)

C. Lion pup with cleft palate, recalling in form the palate of reptiles; showing internal opening of the nose (indicated by the arrow-point) in the forepart of the mouth cavity. In this abnormal specimen the secondary palate has failed to grow over to the midline. (After Keith.)

D. Human embryo at the end of the sixth week, showing the secondary palatal plates beginning to grow in toward the midline and the "primitive choanæ" (arrow-point) still exposed in the forepart of the roof of the pharynx. (After Keith.)

(B, from *Allgem. Zool.*, Gustav Fischer.)

In our survey of the neural part of the human cranium we have seen that its outstanding features are the result of a great cerebral development. When, however, we turn to the facial and pharyngeal parts of the skull and head, we find that the factors which have determined their shape are related to the functions of smell, respiration and of mastication. It is unnecessary to again insist on the fact that the human embryo, in the latter part of the first month, shows a resemblance to a generalized type of fish; it possesses the basis of a branchial arch system. As in the fish, the olfactory organ is represented by a pair of pits or depressions, which at first have no communication with the mouth. In some forms of fish—certain rays and sharks—a channel is formed between each olfactory pit and the mouth. The functional meaning of such a channel is evident; the water imbibed is sampled by the nose before entering the mouth. When pulmonary breathing was introduced, as in Dipnoean fishes, the open naso-buccal channel became enclosed by the union of its bounding folds. In amphibians, reptiles and birds the naso-buccal channel becomes dilated to form a true respiratory nasal passage, and the parts bounding the passage unite on the roof of the mouth to form the **primitive palate.** In Fig. 152 the parts entering into the formation of the primitive palate are shown. They are three in number: (1) a premaxillary and vomerine part developed between the nasal passages; (2) a right and left maxillary part, laid down on the lateral or outer aspect of each passage. In mammals a fourth element is added to the primitive or reptilian palate, and in this way the mammalian mouth is separated from the nasal respiratory passage, and can serve the purposes of mastication and suction. Thus in the evolution of the face there have been three distinct stages: (1) a piscine, in which the nose and mouth were formed independently; (2) an amphibian stage, where the nasal respiratory passage opened on the roof of the mouth; (3) a mammalian stage, in which it opened in the naso-

pharynx. In the development of the human embryo we see these three stages reproduced.

EVOLUTION OF THE TONGUE AND RELATED STRUCTURES

In *Amphioxus* (Fig. 54) there is no tongue and in the lampreys and hags the so-called tongue with its enclosed cartilages probably represents the lower jaw of the shark (Stockard, Goodrich). In the shark the folding up of both the jaw cartilages and the gill cartilages causes the lower ends of the latter to project forward in a series of V's into the floor of the mouth (Fig. 7). These cartilages support the tongue proper, which at first is only a thickening of the floor of the mouth covered with epithelium containing the "taste" cells. In some of the amphibians the tongue becomes highly muscular and protrusile and by the time we reach the lower mammals the tongue is fundamentally the same as that of man. The early primates have a long narrow tongue with a well developed "under tongue" beneath it; in the higher primates, especially the orang, chimpanzee and gorilla, the tongue approaches the human type but is longer in proportion to its breadth. In the detailed number and arrangement of the papillæ

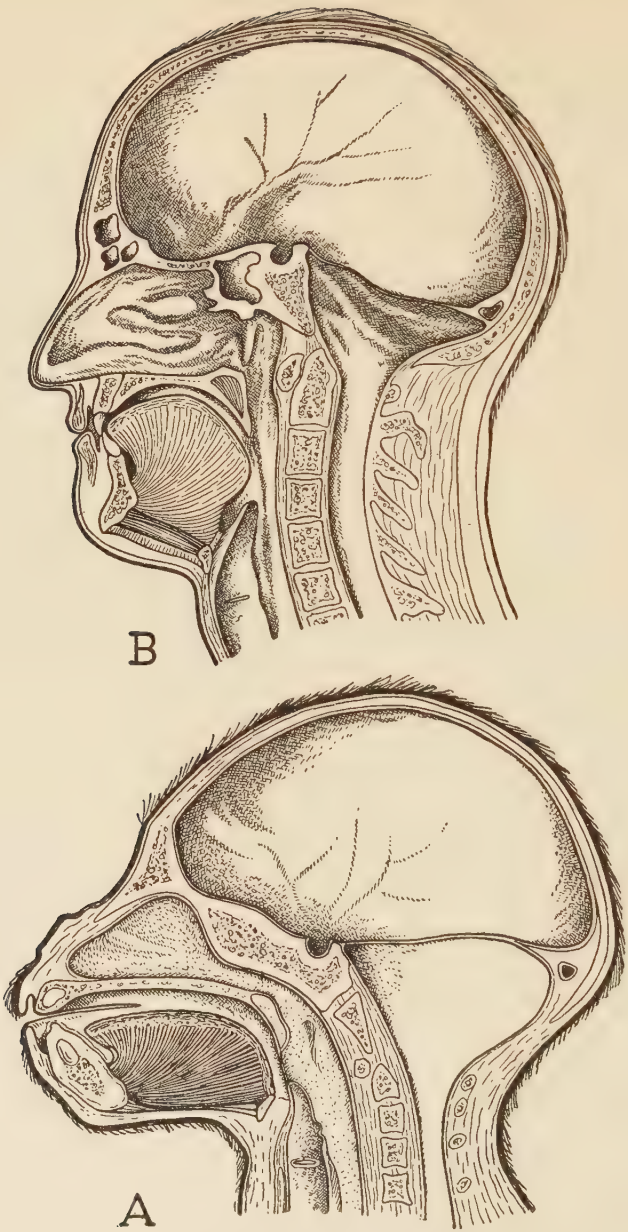

FIG. 67. LONGITUDINAL SECTION OF HEAD IN YOUNG GORILLA (A) AND IN MAN (B), SHOWING RELATION OF TONGUE TO SURROUNDING PARTS (AFTER KLAATSCH).

vallatæ the orang agrees with man (Pocock, Sonntag).

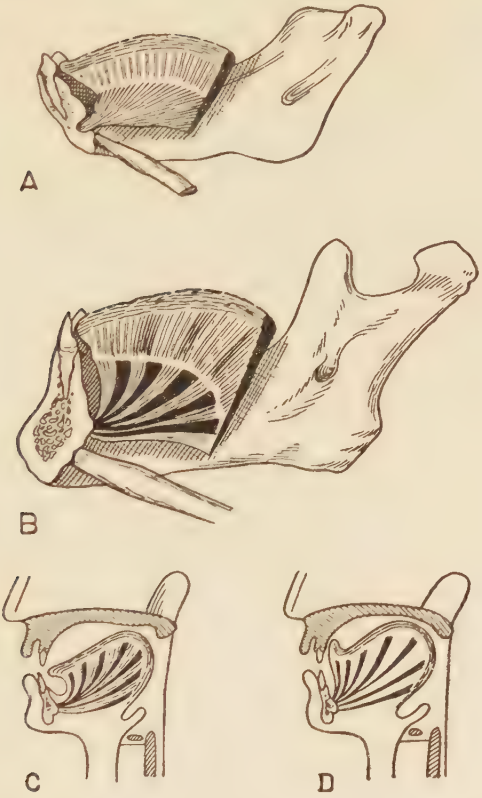

FIG. 68. LONGITUDINAL SECTION OF LOWER JAW OF MONKEY (A) AND IN MAN (B), SHOWING ATTACHMENT OF THE TONGUE MUSCLE TO THE BACK OF THE JAW (AFTER ROBINSON).

C. Diagram of the genioglossus muscle in pronouncing the sound "oo." D. Diagram of the genioglossus muscle in pronouncing the letter "T." (C, D, after Robinson.) For details, see pp. xxviii, xxix.

The muscles of the tongue are the same in the anthropoids and man (Figs. 67, 68) but in the latter

the geniohyoglossus muscles have acquired the ability to change the precise shape and position of the different parts of the tongue with extreme rapidity and in conjunction with movements of other parts of the voice-producing mechanism (Robinson).

The great size of the tongue in man and its important function as the leading organ of speech has doubtless partly conditioned the later stages in the evolution of the lower jaw, especially in the region of the chin, to the back of which the tongue muscles are attached (Fig. 68).

Meanwhile the remaining part of the branchial arches has given rise to the larynx with its highly elaborate voice mechanism, to the tonsils, thyroid and thymus glands, the last two being of vital importance in the normal growth and differentiation of the individual. Again the anti-evolutionist can offer no alternative scientific explanation of the fact that during the course of embryonic development the human tongue, larynx and adjacent structures reveal remarkably detailed resemblances to corresponding structures of lower vertebrates.[1] The "gill-slits" in the human

[1] For a clear presentation of the details see Keith, Arthur, 1921, *Human Embryology and Morphology*, London, pp. 240–252.

embryo (Fig. 69) have been heard of by multitudes, so that certain anti-evolutionists have tried to

FIG. 69. HUMAN EMBRYO OF THE THIRD WEEK (FROM EIDMANN, AFTER HIS).

Oblique front view of the head, showing mouth, primary upper and lower jaw buds, gill arches and gill slits.
(From *Entw. d. Zähne . . .*, Hermann Meusser, Berlin.)

offset their effect by arguing that they are not gill-slits since gills are not present. But this could only confuse people unfamiliar with the evidence that each of the so-called "gill-slits" of the human embryo of the fifth week may be compared directly with a corresponding one in

the fœtal and embryonic stages of other mammals, of reptiles, amphibians and primitive fishes, and that in the fishes these clefts are definitely associated with functional internal gills.

The anti-evolutionists should also be embarrassed by the fact that, leaving the embryonic stages aside, and considering only adult anatomy, the entire complex of the hyoid arch, larynx and associated parts in man corresponds in great detail with those of the anthropoids, differing only in the proportional development of certain parts. From the anthropoids down through the lower primates the homology of every segment of the hyoid arch and laryngeal complex can be completely established and from thence these structures can be traced backward step by step through the reptiles to the lower amphibians and thence to the elaborate branchial skeleton of the crossopt or lobe-finned ganoids. In fact the branchial skeleton of vertebrates, in all its complex relations with the muscles and nerves and in its successive stages of development, affords convincing evidence of the anatomical unity of the entire vertebrate series from shark to man. The human jaws, tongue, larynx and associated parts thus con-

stitute only a single manifestation of a morphological theme that has a thousand variations, but is everywhere patently evolved from a shark-like prototype. And in particular this region yields most cogent evidence of man's unity of origin with the anthropoid apes.

The salivary glands under the tongue and in the sides of the cheek and throat afford another example of the same kind. Huntington has shown how even the variations in man are obviously related to those of the higher primates.

ORIGIN AND EVOLUTION OF THE HUMAN LIPS

Let us return now to the outside of the mouth and consider the origin and evolution of the human lips. The mouth in the lowest existing chordate *Amphioxus* (Fig. 54) is surrounded by short stiff projections. Much the same condition obtains in the larval lamprey (Fig. 59B). In the adult lamprey the mouth cavity is surrounded by a movable ring of cartilaginous plates beset with thorn-like teeth, probably a very specialized arrangement. In the ostracoderms (Figs. 4, 57) of the Silurian the border of the capacious mouth cavity was covered with small scales and plates.

In the modern sharks there is a fold of skin at the back of the upper border of the mouth that seems to foreshadow the maxillary or upper jaw bones of higher fishes (Allis). Underneath this fold of skin at the corner of the mouth are two labial cartilages embedded in muscles which apparently serve to draw forward the corner of the mouth (Fig. 6). A similar fold of tooth-bearing skin (Figs. 50, 53) in the lobe-finned ganoids, or crossopts, gives rise to the premaxillary and maxillary bones, which have every appearance of being homologous with the bones that bear the same name in the earliest amphibians, and from thence these two bones can be followed through the mammal-like reptiles to the earliest mammals, thence through the ascending grades of primates to man. In the earlier crossopts these bones were covered with enamel and lay right on the surface but in the more advanced crossopts the ganoine layer has disappeared and the outer surface of the bone is rough, indicating that it was covered with a thick tough skin. The dentary bone of the lower jaw was likewise covered.

In the early amphibians and reptiles the premaxilla, maxilla and dentary were likewise rough-

ened for the attachment of the outer layers of the skin, of which they themselves formed the deeper layers. In some of the recent reptiles there is a small muscle at the corners of the mouth but the lips are not fleshy and the tough facial mask is not far below the surface. Probably the same conditions obtained in the entire series of mammal-like reptiles.

In the most archaic mammal living today, the Duckbill Platypus of Australia, the mouth is surrounded by a duck-like bill consisting of leathery skin well supplied with sense organs. Very possibly this condition is a specialized remnant of the tough skin that covered the mouth of the mammal-like reptiles. In the Spiny Anteater (*Echidna*) of Australia (Fig. 23C), the nearest living relative of *Ornithorhynchus*, the lips, although peculiarly specialized in connection with the ant-catching, protrusile tongue, approach the normal mammalian condition in so far as they are supplied with muscles that are innervated by the seventh or facial nerve and are covered with hair rather than scales.

Here we arrive at the most distinctive feature of the lips of mammals, in which the bony mask

inherited from the primitive crossopts lies deeply covered by a mobile fleshy curtain. Doubtless the evolution of true lips was a part of the general transformation of reptiles with unstable body temperature and low grade metabolism, into mammals living at high pressure.

In an earlier chapter (pages 43, 44) it has been mentioned that the facial muscles of mammals represent a forward extension of a thin layer of muscle covering the neck of lower vertebrates and that when this muscle migrated forward beneath the skin it dragged its own nerve with it, which was subdivided into smaller branches as the muscle itself was differentiated into the facial muscles of the ears, eyes, nose and lips (Figs. 23, 24). The history of this invasion is now being traced in convincing detail by Huber. The invasion was facilitated by the fact that in the early stages of development (Figs. 65A, 69) the region of the mouth and lips arises quite close to the original territory of the facial nerve, which was on the side of the neck, so that forks of the parent mass in the neck could easily spread to the lips and forehead.

The researches of Ruge, Huber, Sonntag and

Fig. 70. Old Chimpanzee, Showing Extraordinary Protrusion of the Lips in Anthropoids.

(From J. A. Allen, from a photograph by Herbert Lang.)

others have shown that the anthropoids (as usual) are man's nearest living relatives in the anatomy of the facial muscles. The ability to move the ears is already reduced in the anthropoids but some men can still make a creditable showing of activity in these souvenirs of man's earlier mammalian ancestors.

In the lower primates the opposite upper lips, like those of carnivorous mammals, depend slightly at the sides and are barely, if at all, joined in front, but in the anthropoid apes and man the median flap of the fœtus, forming the philtrum of the lip in adult man, becomes very broad, so that the opposite halves of the orbicularis oris muscle become broadly continuous.

Thus the anthropoids acquired highly protrusile lips, useful in sucking up water and the juices of fruit (Fig. 70). *Man has inherited from the primitive anthropoids the ability to draw back his lips in anger, to open them in a laugh, or again, to protrude them into a funnel and so to confer kisses on the objects of his affection.* How much dour literature, ancient and modern, might be lightened by this thought!

All these muscles of the mouth and cheeks as

well as the muscles of swallowing were naturally of vital importance to the newborn mammal, enabling it to pump the mother's milk into its swelling cheeks. But how long it took mankind to realize the deep significance of the fact that even babies of bluest blood share this birthright with the beasts of the field.

LATER STAGES IN THE HISTORY OF THE TEETH

Thanks to the advertisers of tooth pastes all America knows the practical importance of beautiful teeth. But few indeed share the secret as to how we obtained these dazzling objects of charm, and fewer still ever give a thought to the humble creatures who slowly shaped them to our use. It is surprising that even today, after hundreds of millions of years' advancement beyond our shark-like ancestors, each human being, during the embryonic development of his teeth, starts at a shark-like stage (Fig. 71A). For at first the area of embryonic skin that is destined to give rise to the teeth lies on the surface of the mouth cavity, then it sinks down like a pouch (Fig. 71B), the bottom of the pouch is pushed upward (Fig. 71C) to form a pulp cavity and thus the germ of the

human tooth becomes essentially like the germ of the shark's tooth. However, in order to defend

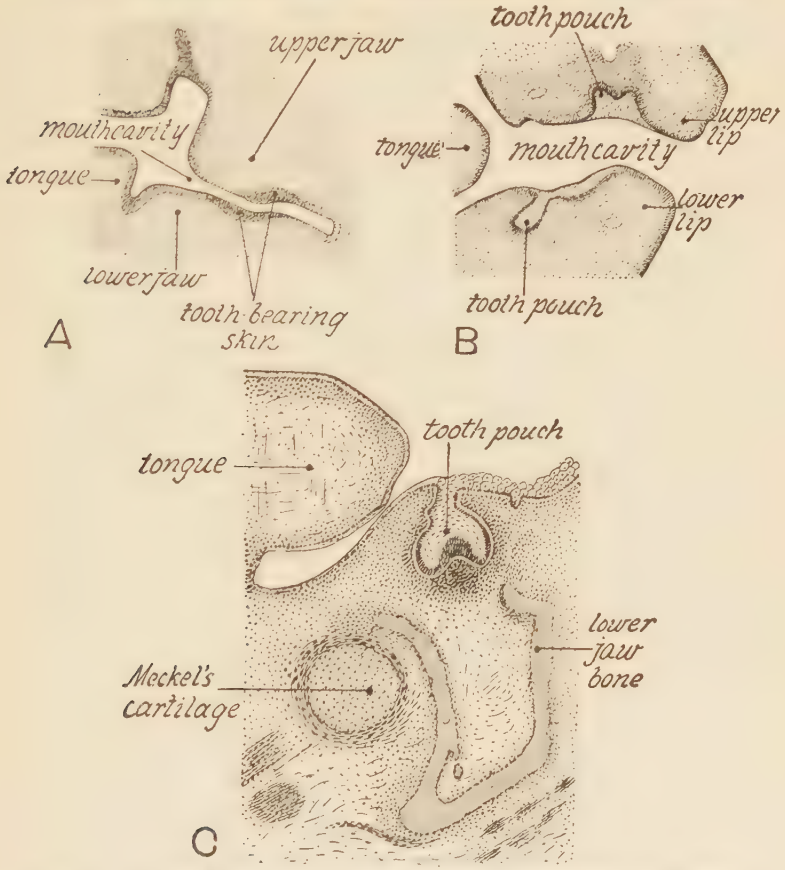

Fig. 71. Three Embryonic Stages in the Development of Human Teeth (A, B, from Eidman after Ahrens; C, after Corning).

(A, B, from *Entw. d. Zähne . . .*, Hermann Meusser, Berlin; C, from *Lehrb. d. Entw. des Menschen*, J. F. Bergmann.)

For details, see p. xxix.

the validity of these comparisons it is essential to note that we are not leaping at once from shark

to man in the reckless manner of some of the older comparative anatomists, but that the same general process of tooth development may be traced in many successive grades in the ascent from fish to man.

Meanwhile (Fig. 71C) Meckel's cartilage, the descendant of the primary lower jaw of the shark, lies entirely free from the future dentary or lower jaw bone, which will later surround both the Meckel's cartilage and the developing tooth-germ, as in all the vertebrates above the shark.

In the earlier creatures that lie in or near the line of ascent to man the teeth were of the dog-tooth or canine type (Fig. 50). Some of the front teeth of man, especially the cuspids or canines, remain single-cusped to this day as souvenirs of our remote carnivorous ancestors; but the central incisors often exhibit a tendency to develop little cusps, mammillæ or subdivisions, along the flattened cutting edge of the crown (Fig. 72). The frequent presence of these mammillæ on the edges of the central incisors has sometimes been cited as evidence of a "triconodont" stage in the evolution of human teeth, in disregard of the fact that not even the extinct triconodont mammals of the

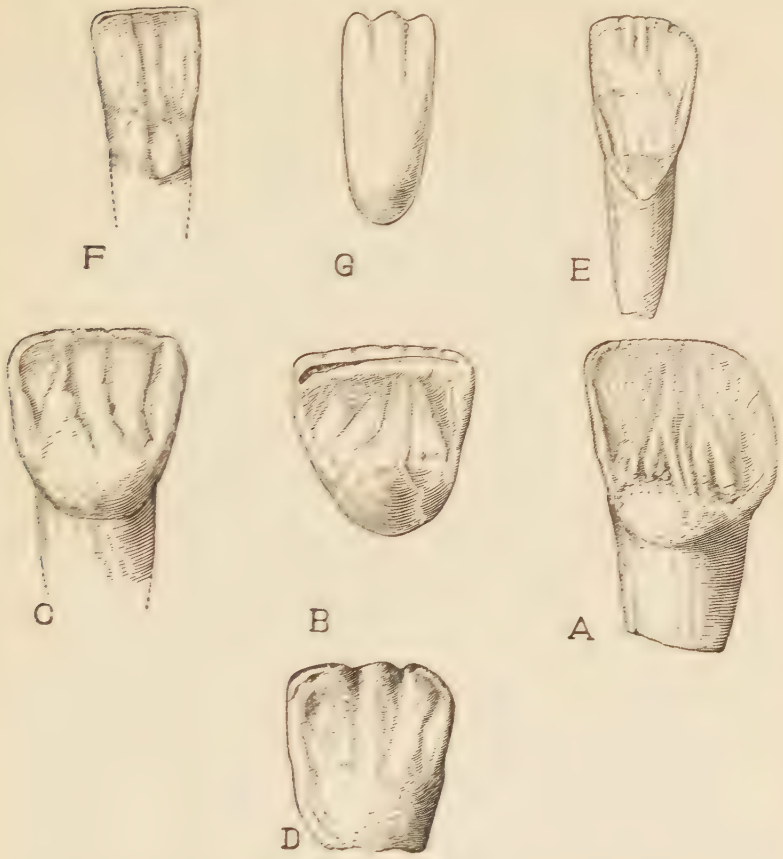

FIG. 72. CENTRAL INCISORS OF GORILLA (A, E) AND MAN (B, C, D, F). ENLARGED. (B, AFTER WEINERT, C. F, AFTER VIRCHOW; D, AFTER HRDLIČKA; G, FROM HRDLIČKA, AFTER ZUCKERKANDL.)

For details, see pp. xxix, xxx.

Triassic age themselves had "triconodont" incisors but only triconodont molars. In whatever way this tendency to subdivide the central incisor

edges may have arisen, man shares it with many other mammals, especially with his relatives the anthropoid apes, whose central incisor crowns approach the human type. Remane (1921, Fig. 21E) has shown that in certain chimpanzees even the outer rim of the central upper incisor is vertical as in man.

Hrdlička has noted that on the rear surface of the central upper incisors of certain anthropoids and monkeys one finds the "rim and ridge" formation (Fig. 72) of many human incisors.

In the upper central incisors of recent Mongolians and many Indians the rims along the sides of the crown fold around toward the rear and the "shovel-shaped" incisor is developed. This arrangement was already foreshadowed in certain gorillas and is almost fully attained among the extinct Neanderthals of the Krapina race; it has also recently been discovered in a fossil human tooth from the Pleistocene of China. In its extreme form the shovel-shaped incisor represents a distinct specialization beyond that attained in the anthropoids. Dr. J. Leon Williams has observed among all races of mankind the presence of three types of central upper incisors (Fig. 73).

In the first type the inner and outer borders of the crown as seen from in front tend to be straight and vertical: in the second type the opposite borders diverge sharply toward the lower end of the crown; and in the third the outer border has a

Fig. 73. The Three Types of Central Upper Incisors (after J. Leon Williams).

Lower row, first type; middle row, second type; upper row, third type.

marked double curve. Exactly these same three variants he found also in all the existing species of anthropoid apes and he rightly considers that this fact, taken in conjunction with hundreds of other items of similar purport, affords decisive evidence of close kinship between man and anthropoids.

The upper lateral incisors in anthropoids (Fig. 74) as a rule are more primitive in retaining the

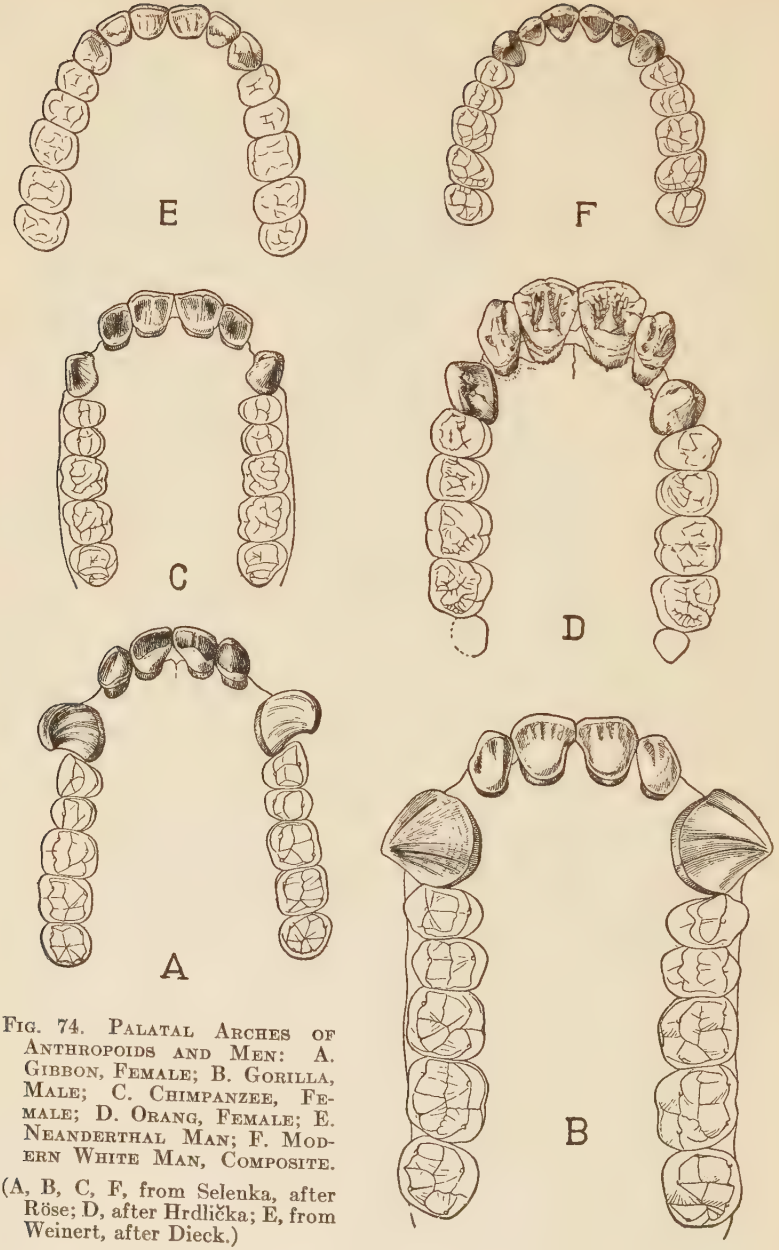

FIG. 74. PALATAL ARCHES OF ANTHROPOIDS AND MEN: A. GIBBON, FEMALE; B. GORILLA, MALE; C. CHIMPANZEE, FEMALE; D. ORANG, FEMALE; E. NEANDERTHAL MAN; F. MODERN WHITE MAN, COMPOSITE.

(A, B, C, F, from Selenka, after Röse; D, after Hrdlička; E, from Weinert, after Dieck.)

bluntly pointed tips, but Remane (1921, page 102) figures a certain chimpanzee in which the tip of the lateral upper incisor is submerged in a transverse incisal edge and even the outer rim is vertically developed, so that the crown as a whole is clearly approaching the human type.

The great outstanding difference between the dentition of man and that of his anthropoid cousins lies in the fact that in man the canine teeth, even in the milk set (Fig. 76) are much reduced in size, with rounded crowns and obtuse tips that project but little above the level of the adjacent teeth, while in the anthropoids, especially the males, the canines form large sharp-tipped tusks. If, however, the fossil lower jaw found at Piltdown, England (Fig. 45C), belongs with the human Piltdown skull, as nearly all authorities now believe, it affords a clear case of an ape-like canine belonging in a human jaw; only it should be noted that the Piltdown canine is much more like the lower canines of certain female gorillas, which have not attained the tusk-like stature of male canines. The human canines may indeed be most reasonably regarded as reduced and "infantilized" or "feminized" derivatives of a

primitive anthropoid type and the process of reduction and infantilization may well have taken place during the millions of years of the Lower Pliocene epoch, at a period when the fossil record of human remains so far discovered is still blank.

The great mass of collateral evidence for the derivation of man from primitive anthropoids with well developed but not greatly enlarged canines, has been reviewed lately with great thoroughness by Remane, who finds no justification for the view that man has avoided the primitive anthropoid stage and has been derived from wholly unknown forms with the canine tips not projecting much beyond the level of the premolars.

When the skull of a chimpanzee (Fig. 35F) and the skull of a high type of man (Fig. 43D) are viewed from above, the ape is seen to differ widely from man in the marked projection of his muzzle. This projection is less in female anthropoids with smaller teeth and still less in early fœtal anthropoid stages before the tooth-germs are formed. On the other hand, savage types of man with very large teeth have a correspondingly prominent muzzle, especially if the molar and premolar teeth have large fore-and-aft diameters, as in the fossil

Talgai, Australia, skull (Fig. 42E), which has a strongly protruding muzzle. Again, the Piltdown lower jaw (Fig. 45C) with its "simian shelf" in front, its female anthropoid canine and its ape-like molar teeth (Fig. 41A), must indubitably have had a muzzle approaching that of an immature female gorilla. By the time we reach the Heidelberg and Neanderthal fossil men, however, the canines had become reduced to the level of the cheek teeth, the incisors and premolars were reduced in size and the lower molars were relatively wider than in the anthropoids; hence Professor McGregor's very thoroughly studied restorations show these men with only moderately developed muzzles and human lips.

The reduction of all the front teeth in man is foreshadowed in the fœtal stages in which the tooth-germs are smaller than those of apes; consequently the fœtal muzzle is likewise smaller than that of fœtal apes of corresponding stages.

The reduction in size of all the teeth, especially the canines, has been an important factor in shortening the palatal arch (Fig. 74) from the long ∩-shaped type of anthropoids, with a wide space between the canines, to the short human

form of palate with narrow space between the canines. In the lower jaw the diminution of the lower canines and the backward retreat of the incisors finally brings the canines almost to the

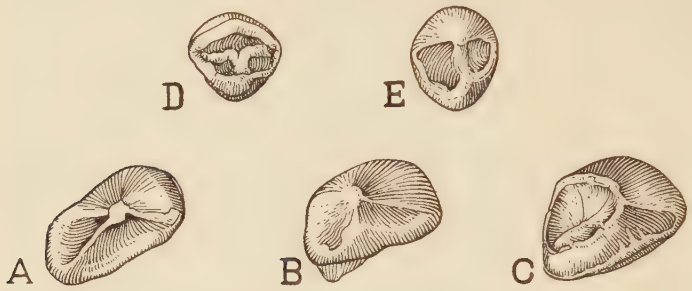

Fig. 75. Lower Front Premolars of Fossil Anthropoids (A, B, C) and Man (D, E).

(A, B, after Gregory and Hellman; C, after Pilgrim; D, after Virchow; E, from Selenka, after Röse.) For details, see p. xxx.

front of the jaw and into functional alignment with the incisors.

The upper premolars or bicuspids of man, which in the adult dentition are two in number on each side of both the upper and lower jaws, find their nearest relatives in the bicuspid upper and lower premolars of the anthropoid apes (Fig. 74).

The front lower premolars of the anthropoids show a wide range of forms, from types with a more compressed baboon-like crown to the almost human premolars of the extinct *Sivapithecus* (Fig. 75C)

and of certain modern chimpanzees. Remane records the fact that in certain human jaws the front lower premolar retains clear vestiges of the asymmetrical form of the outer surface of the crown, a condition that is far more accentuated in the typical anthropoids and is there associated with the large size and tusk-like form of the upper canines.

Neither the upper nor the lower molars of man show much resemblance to those of the cynodonts or pro-mammals of the far-off Triassic age (Fig. 77I); yet we owe to such lowly forbears the initial phases of the process by which the simple dog-tooth crowns of the cheek teeth began to subdivide and give rise to the accessory tips or cusps that are so characteristic of the cheek teeth of mammals.

Anti-evolutionists ask us to believe that even the hairs of our head are numbered, but we affirm only that our teeth are numbered: twenty in the milk set and thirty-two in the permanent sets of normal individuals; and that the same numbers occur in the anthropoid apes; that typical representatives alike of mankind and of the apes, have in the permanent dentition two incisors, one canine, two premolars, three molars, on either side in both

the upper and lower jaws; and in the milk set, two incisors, one canine and two milk molars on either side above and below (Fig. 76).

The history of the human upper and lower premolar and molar teeth (Figs. 77, 78) has been

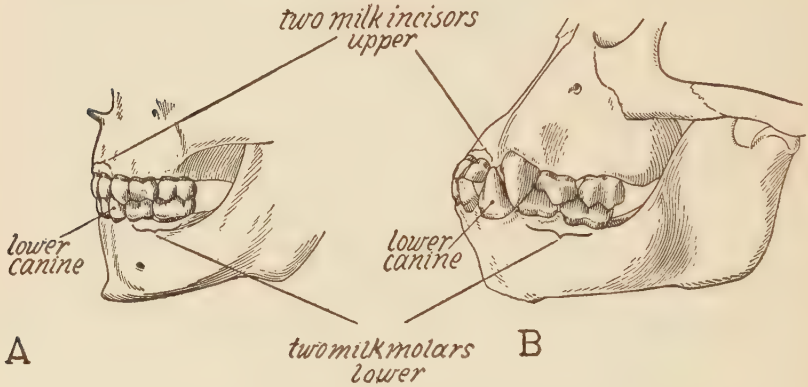

Fig. 76. Milk Teeth of Man (A) and Gorilla (B). (Both from Selenka, after Röse.)

discussed at length by myself in the work on the *Origin and Evolution of the Human Dentition* and other papers and by Gregory and Hellman in our work on *The Dentition of Dryopithecus and the Origin of Man.* We have shown that notwithstanding the present profound differences in habits between man and the anthropoid apes, the lower molar teeth, especially of more primitive and more ancient races of man, retain the most

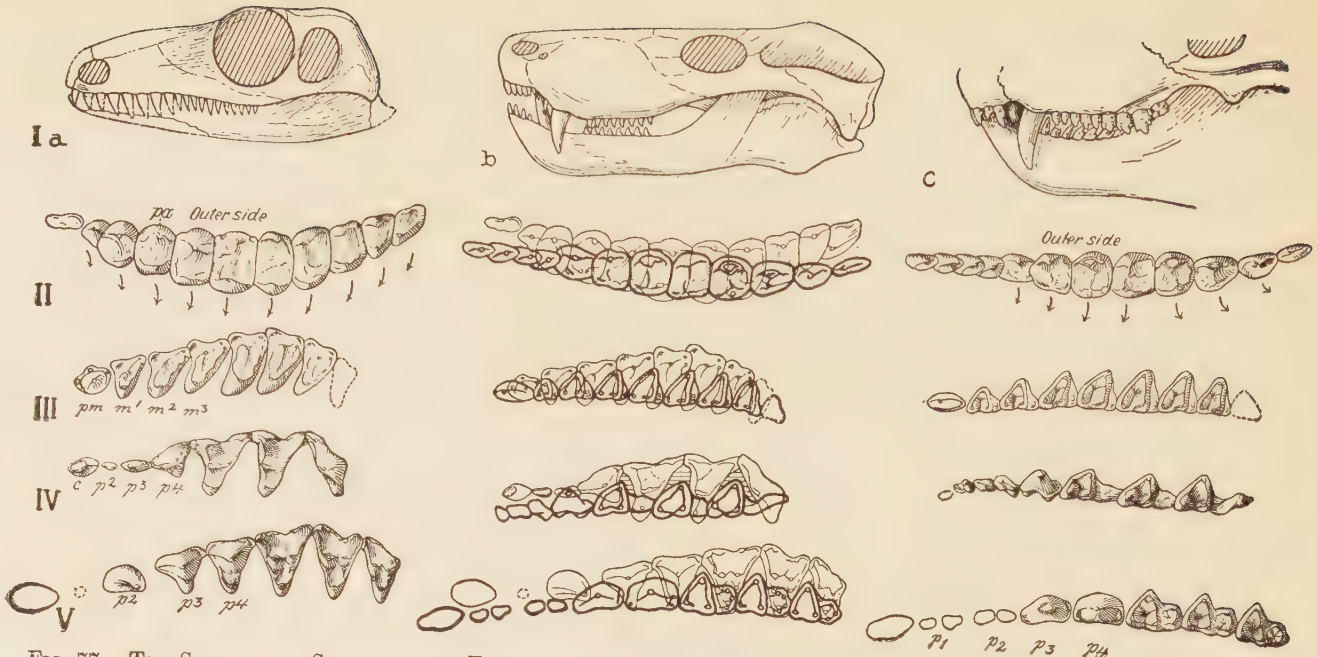

FIG. 77. TEN STRUCTURAL STAGES IN THE EVOLUTION OF THE HUMAN DENTITION FROM ASCENDING GEOLOGICAL HORIZONS.

Ia. Primitive theromorph reptile (after Williston). Ib. Primitive mammal-like reptile (after Broom). Ic. Advanced mammal-like reptile (after Seeley). II. Advanced mammal-like reptile (mainly after Seeley). III. Primitive pro-placental (kindness of Dr. Simpson). IV. Pro-trituberculate (from original specimen). V. Primitive placental (from original specimen).

For details, see p. xxxi.

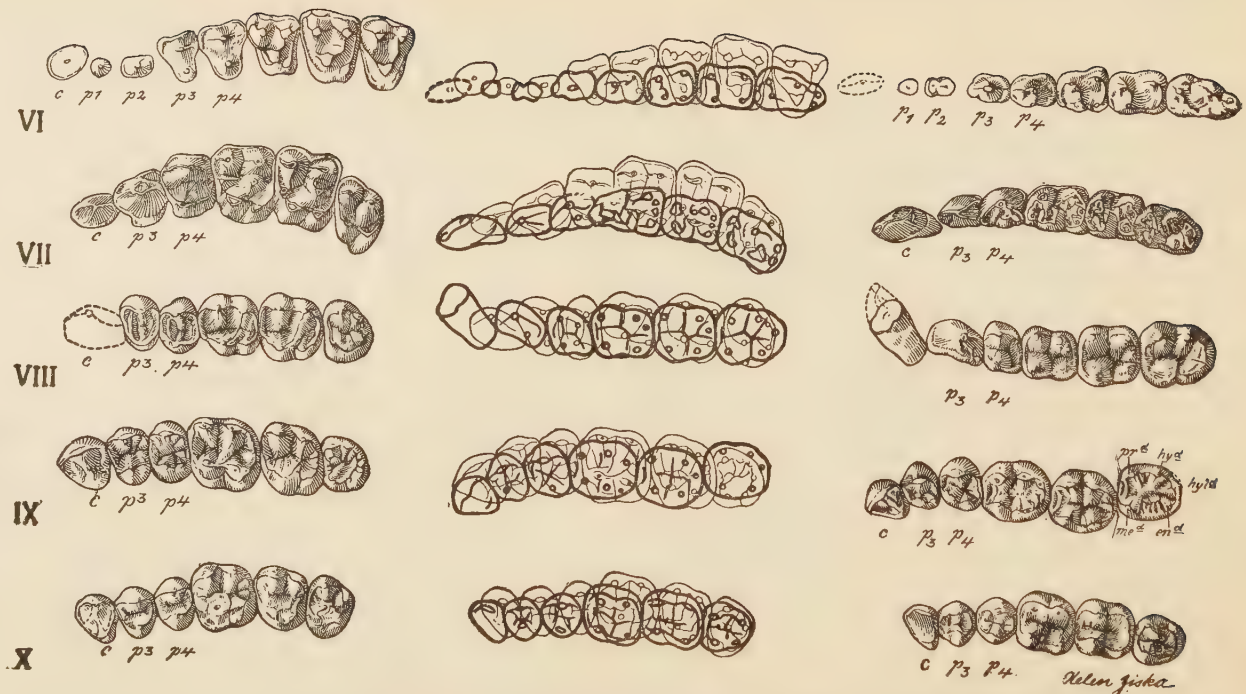

FIG. 78. TEN STRUCTURAL STAGES IN THE EVOLUTION OF THE HUMAN DENTITION (*Continued*).

VI. Primitive primate (after Grandidier). VII. Advanced tarsioid primate (after Stehlin). VIII. Primitive anthropoid primate (upper molars mainly after Pilgrim). IX. Primitive man, Mousterian (from stereoscopic photographs by McGregor and published photographs by Weinert and by Virchow). X. Modern man, white (from original specimen).

For details, see pp. xxxi, xxxii.

indubitable marks of anthropoid kinship and derivation; the lower molar crowns displaying many intermediate stages from an almost perfect "*Dryopithecus* pattern" (Fig. 80C) with five main cusps and a complex, definite system of grooves and depressions, to a "cruciform," four-cusped form in which the *Dryopithecus* pattern is largely obliterated (Fig. 80F).

Similarly the upper molar crowns of the fossil Neanderthal skull known as "Le Moustier" (Fig. 78IX) may be compared cusp for cusp and ridge for ridge with those of such fossil anthropoids as *Dryopithecus rhenanus* of Europe and *Sivapithecus* of India, both of which even possess the peculiar depressions known as the fovea anterior and fovea posterior, which are characteristic of primitive human upper molars. Here again, as in the case of the lower molars, it is only the more primitive members of the human race that retain such indubitable traces of anthropoid kinship, the conditions of civilization tending to reduce the vigorous upper molar pattern of the primitives to an enfeebled type with less robust cusps and less salient angles (Fig. 78X).

Similarly the entire set of milk teeth of man

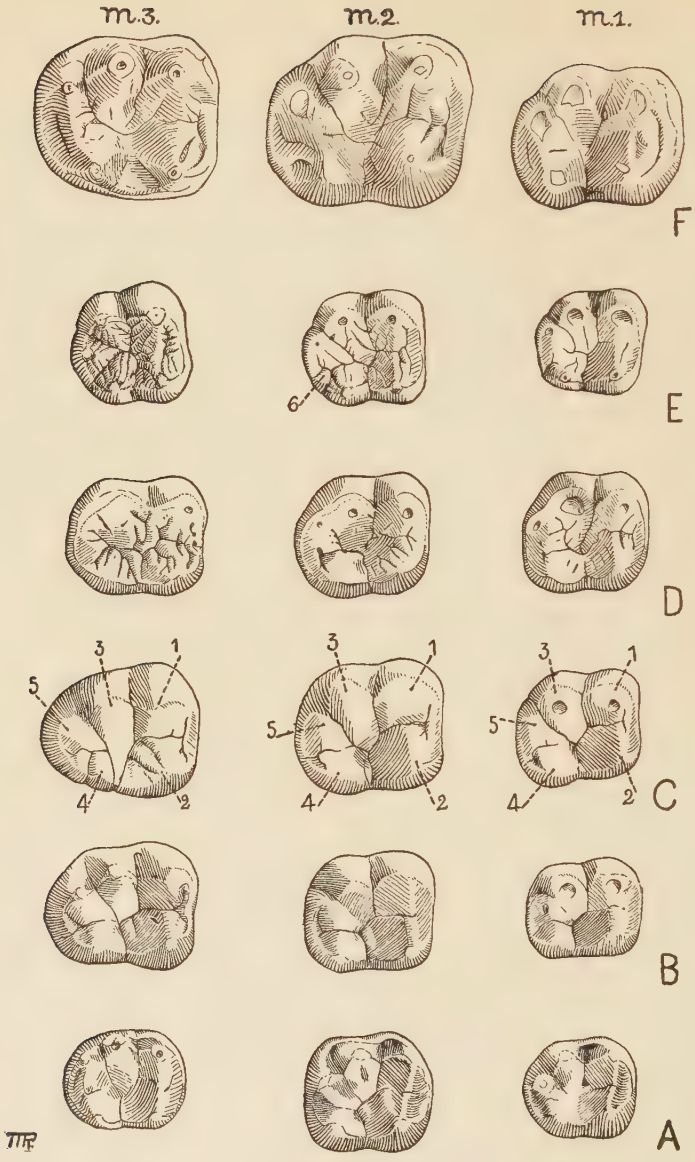

Fig. 79. The *Dryopithecus* Pattern in the Lower Molar Teeth of Fossil (A, B, C) and Recent (D, E, F) Anthropoids.

For details, see p. xxxii.

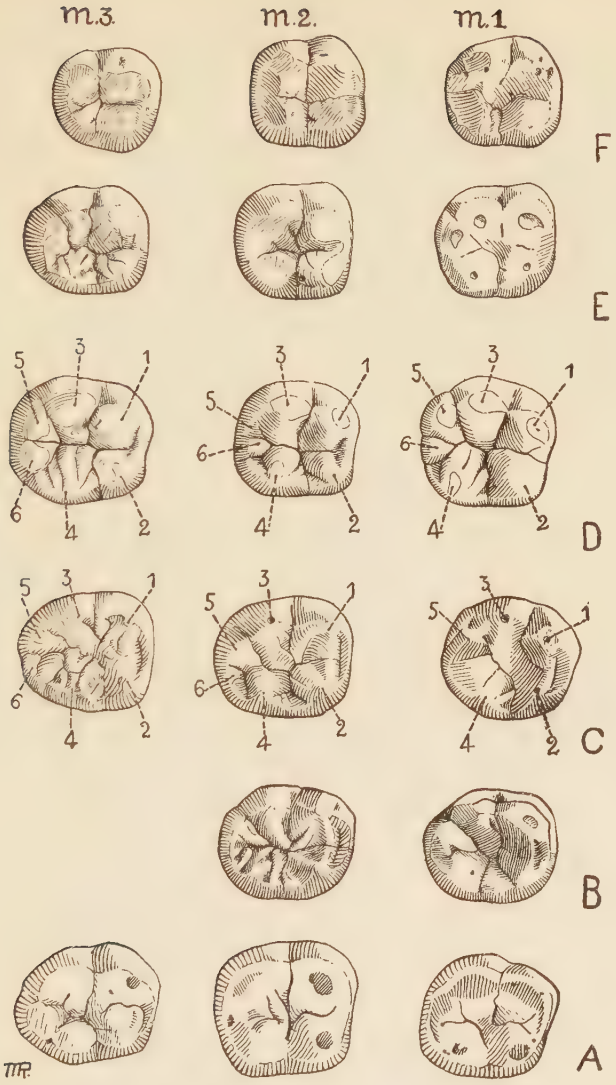

FIG. 80. PROGRESSIVE REDUCTION AND LOSS OF THE *Dryopithecus* PATTERN IN THE LOWER MOLARS OF FOSSIL (A, B, C) AND RECENT (D, E, F) MEN.

For details, see pp. xxxii, xxxiii.

must be regarded from a scientific viewpoint as derived by a few easily understandable modifications, from the type exemplified in the young of recent anthropoids (Fig. 76).

Against all this mass of evidence for man's evolution from a primitive anthropoid stock the modern schoolmen can only quibble that the corresponding parts of man and ape are "equivocable" but not "homologous."

CONCLUSIONS

Perhaps the most important and basic conclusion concerning the early history of the mouth and jaws in the remote ancestors and predecessors of man is, first, that however the mouth and jaws may have arisen in the first place, their subsequent history, from the grade of organization represented by the shark, may be traced through to man in its broad outlines with the greatest security; secondly, that whatever may have been the food habits of the invertebrate ancestors of the vertebrates, it is extremely probable that from the shark grade onward to the early mammalian ancestors of man, the mouth and jaws were adapted for the capture and disposal of sizable living prey and not for

the manipulation of any less nutritious form of food.

The amelioration of our features we owe not so much to the savage, furry little beasts that first bore the name of mammals, nor even to the earlier primates, who despite their large eyes and large brains still retained a fox-like snout and long jaws; but chiefly to the gentle pro-anthropoids who first took to a diet of fruit and buds and so acquired many modifications of the lips, jaws and dentition, which they transmitted to the earlier and less progressive races of men.

How much arrogance, deceit and wickedness would have been spared the world, if men had realized that even the most imposing human faces are but made-over fish traps, concealed behind a smiling mask but still set with sharp teeth inherited from ferocious pre-mammalian forbears.

History of The Nose

Why do all men, anti-Darwinians included, have noses? Why does the human nose, both externally and internally, have precisely the same parts, only differently proportioned, as the noses of the gorilla and the chimpanzee? Why are man and ape,

in this feature as in thousands of others, created so nearly in the same image? "Parallelism" say the anti-Darwinians; but physiology, comparative anatomy and allied sciences answer, "Blood kinship."

The story of the early evolution of the human nose would be strong reading for the delicate stomachs of our Mid-Victorian lady relatives. But in these Neo-Elizabethan days we will not shudder unduly at the thought that noses, at least of the vertebrate type, were first created in order to lead our shark-like ancestors straight to the feast—some nameless horror wallowing in the uneasy tide and alive with the writhing creatures that consumed it. Even to this day, odors cannot reach us except in water vapor.

The shark's smelling apparatus is comparatively simple—an extended surface of membrane sensitive to olfactory stimuli, folded into a rosette and packed neatly into the olfactory capsule, one on each side of the head. A small opening, the nostril, admits the water to be tested, and a groove, the oronasal groove of primitive sharks (Fig. 66A), connects the nose with the mouth cavity. In the embryo shark and embryo mammal the nasal sac

begins as an out-pushing of the mouth cavity, of which it thus appears to be only a specialized outgrowth for the detection and testing of food.

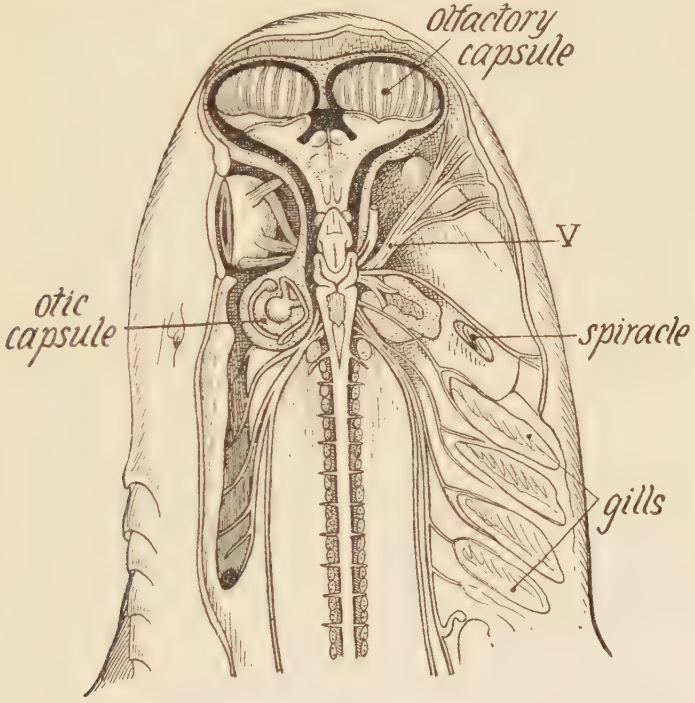

Fig. 81. Dissection of Head of Shark, Seen from Above, to Show Relations of Olfactory Capsules to Brain, Eyes and Internal Ears (Modified from Marshall and Hurst).

The most essential parts of the nose are the olfactory sense organs and the olfactory nerve. The fibers of the latter are spread all over the olfactory membrane, from which, being collected into two great nerve cables (Fig. 81), they pass

backward into the forebrain, of which indeed they form the dominant part. If favorable signals are transmitted by the smelling nerves, the eyes turn toward the source of the odor and by means of the locomotor machinery the whole "ship" is steered in the right direction. The two olfactory capsules, rather widely separated from each other on either side of the head, not only double the chance of picking up a trail of olfactory value, but doubtless also serve as directional organs. The bilateral arrangement of the other sense organs may have a similar significance.

The resemblances of the shark nose to the human nose are fundamental and the subsequent changes in this organ are relatively not great. The ultimate mystery with regard to all the sense organs of vertebrates is decidedly not what are the broad stages of their evolution from fish to man, but what physical and chemical forces acting upon the primitive vertebrate skin caused one set of epithelial cells to become sensitive to olfactory stimulations, another set to respond to light, others to physical vibrations of different rates, and still others to be deaf and blind to all other stimuli except those coming from within the organism;

and what now causes other cells of the same primary outer layer to become a line of olfactory nerve cells, attached to the sense organ and arising from a nucleus in the central nervous system. Experimental embryology and physiology of the future may reveal some of the chemical changes involved, as the generalized ectoderm cell differentiates into the specialized one capable of only one class of reactions; but this will only widen our knowledge of the bewildering complexity of the single fertilized egg cell, which divides and subdivides so as to give rise to the olfactory organs as well as to all other parts of the body.

Meanwhile, as stated above, the main transitional stages in the evolution of the nose from fish to man are fairly well understood, and are well described in Keith's *Morphology and Embryology*. First the olfactory sac becomes folded up, and in sharks a groove (Fig. 66A) extends downward toward the corner of the mouth. Second, in the lung-fishes this lower extension of the sac has worked its way inside the mouth and there are thus two openings, a nostril on the outside and an internal narial opening in the roof of the mouth. Third, both in the air-breathing fishes and the

amphibians air may either be gulped in through the mouth or sucked in through the nose, which thus functions in breathing as well as in smelling.

By the time we reach the mammal-like reptiles of the Triassic of South Africa (Fig. 53VI) we find the paired olfactory capsules greatly elongated in a fore-and-aft direction, and in the highest members of this series, as shown by iron-stone casts of the interior of the nasal chamber, the median bony partition now supported scroll-like outgrowths like the delicate turbinate bones of mammals (Watson). The delicate olfactory membrane thus spread out on these scrolls, which in many mammals become complicated with secondary scrolls, thus secures a wide surface for testing the odors of the air drawn in.

In the living amphibians, reptiles and more primitive mammals there is also a pair of small cartilaginous scrolls near the bottom of the median cartilaginous partition, which contains a folded pocket of the olfactory membrane; from this pocket a very fine tube leads downward, opening into the cavity of the mouth. This whole arrangement is called Jacobson's organ. Primitively Jacobson's organ seems to have served for the

testing by the olfactory membrane of the contents of the mouth, while the main portion of the olfactory membrane served to test the inspired air in the main chamber. In the marsupials and other lowly mammals Jacobson's organ is comparatively well developed but in the higher primates and especially in man it is either absent in the adult

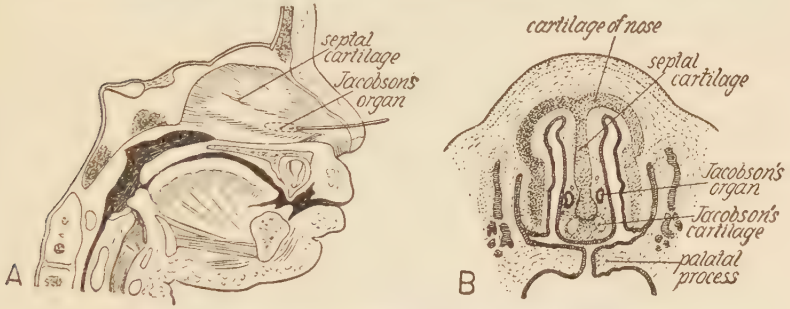

Fig. 82. Jacobson's Organ in the Human Fœtus.
(After Corning.)
(From *Lehrb. d. Entw. des Menschen*, J. F. Bergmann.)
For details, see p. xxxiii.

stage or it exists in a vestigial and, so far as known, a useless condition. It is present, however, in the early fœtal stages of man (Fig. 82), degenerating later. Here then is another "poser" for anti-evolutionists. Is the fœtal human Jacobson's organ made after a divine prototype? And is the same true of the vestigial Jacobson's organ of the Old World monkey? Or have both man and monkey received this now vestigial or fœtal struc-

ture as part of their heritage from far earlier mammals in which it was more fully developed?

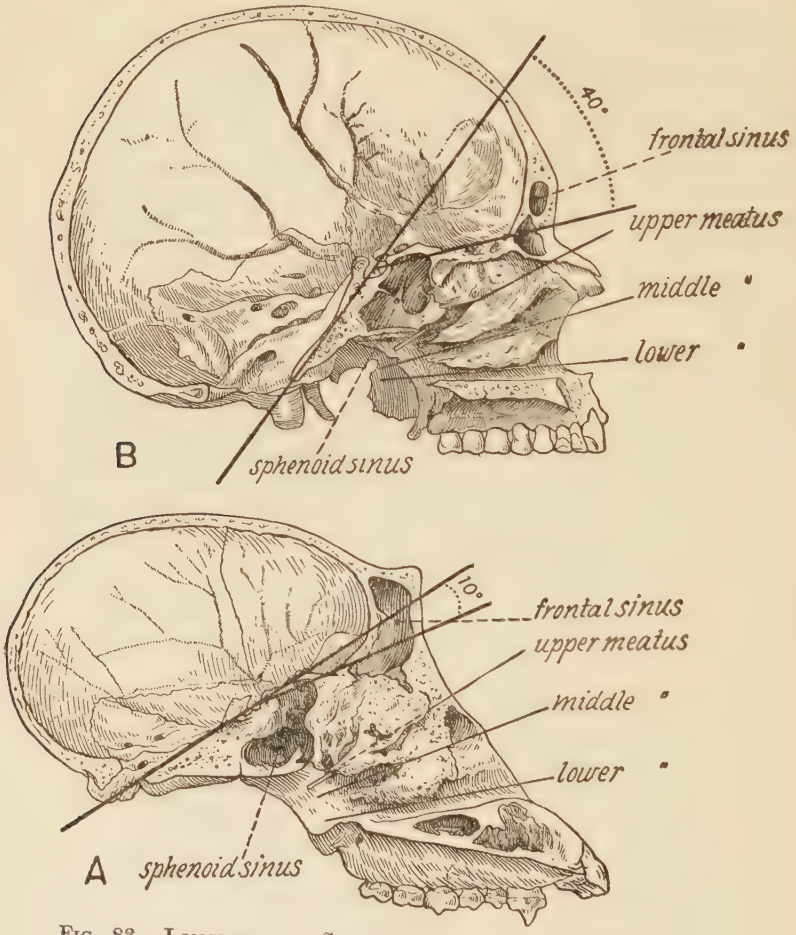

FIG. 83. LONGITUDINAL SECTION OF THE SKULL IN MAN (B) (AFTER CUNNINGHAM) AND CHIMPANZEE (A).

A similar dilemma might politely be offered to anti-evolutionists with regard to the whole anatomy

of the olfactory chamber. Why is it that man agrees with the Old World monkeys and anthropoid apes in the numbers and arrangement both of the turbinate scrolls that arise from the median partition or septum and of those that spring from the inner wall of the upper jaw bone? In man

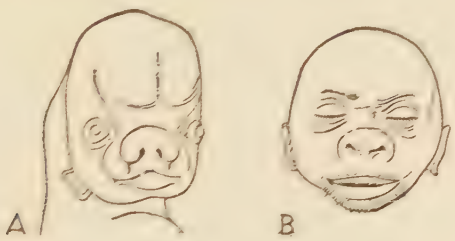

FIG. 84 BROAD FORWARDLY-DIRECTED NOSE OF HUMAN FŒTUS (A) (AFTER KOLLMANN) AND GORILLA FŒTUS (B) (FROM SCHULTZ, AFTER DENIKER).

these delicate bony scrolls, deeply buried in mucous membrane, are arranged in such a way that three air passages, the upper, middle and lower meati, pass between the scrolls and allow the air to pass downward and backward to and from the pharynx. In the Old World monkeys and anthropoid apes the same passages are present as in man, but in the chimpanzee and the gorilla the resemblance to man is even more striking, since the air cavities or sinuses in the frontal,

ethmoid and sphenoid bones have similar tubular connections with the nasal meati (Keith).

Nor should the anti-evolutionist be any less embarrassed by the history of the embryonic development of his own nose in comparison with that of other animals. For, broadly speaking, the human nose passes through an early stage in which the olfactory capsule is undeniably like that of a fish (Fig. 65); then the lower end of the capsule is prolonged downward in a tube which opens into the roof of the mouth; at this stage the morphology of this region is substantially like that of an amphibian or of a reptile; then horizontal plates (Fig. 66D) grow out from the upper jaw to form a secondary bony palate, so that the mammalian grade is reached in which the inspired air is delivered into the pharynx back of the palate.

Meanwhile the membranous Eustachian tube has sent off bubble-like outgrowths (Fig. 85), which invade the frontal, ethmoid, sphenoid and superior maxillary bones, forming in them the complex system of sinuses and antra which in its entirety is peculiar to man and the higher anthropoid apes (Keith).

With regard to the external nose, neither the

comparative anatomy nor the embryonic development of this region give the slightest support to those who stress the isolation of man. On the contrary, they show quite conclusively that man and apes are merely the divergently modified derivatives of a common pro-anthropoid stock and

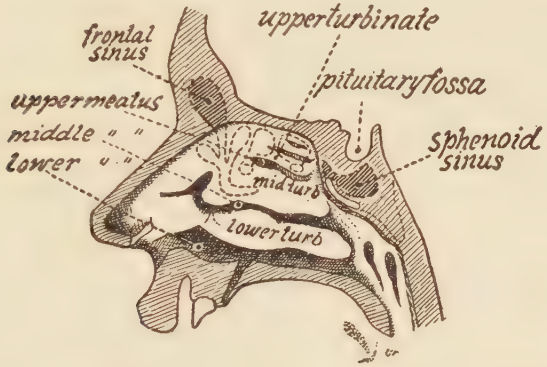

Fig. 85. Connections of the Frontal, Ethmoid and Sphenoid Sinuses with the Nasal Meati (after Keith).

that with regard to this region civilized man has become much further modified away from the primitive ancestral condition than either the gorilla or the chimpanzee.

In earlier human stages of development (Fig. 86) the nostrils are widely separated, almost as in the South American monkeys. Later (Fig. 86E) the opposite halves of the nose grow together. At this stage the nose is very wide in proportion

to its height and as a whole is essentially indentical (Fig. 84B) with that of fœtal chimpanzees and gorillas. This fact, together with a multitude of similar ones, establishes the relatively close relationship between man and the existing anthropoids; it also indicates that in the shape of its nose the common ancestor of man and the anthropoids was far more like a gorilla than like a white man.

According to Professor Schultz, even unborn fœtuses show wide differences in the form of the nose, but in general, babies have wide short noses with very low bridges. In the negro pygmy represented in Fig. 89A the nose has remained in a low stage of fœtal development (*cf.* Fig. 86D). In the Mongolian race the infantile form of nose tends to be retained in the adults. How then does one baby grow up to have the famous figure-6 Jewish nose, another the V-shaped Alpine nose? How did that pretty British girl acquire a nose which has just the suspicion of an upturn at the tip? Why do exceedingly tall men have very long noses? Why do fat men often have inadequate juvenile noses? Of course it seems like a truism to say that in thin sharp noses the vertical components of growth of the nasal septum have

far outstripped the transverse components of the nose as a whole; yet such no doubt are the most

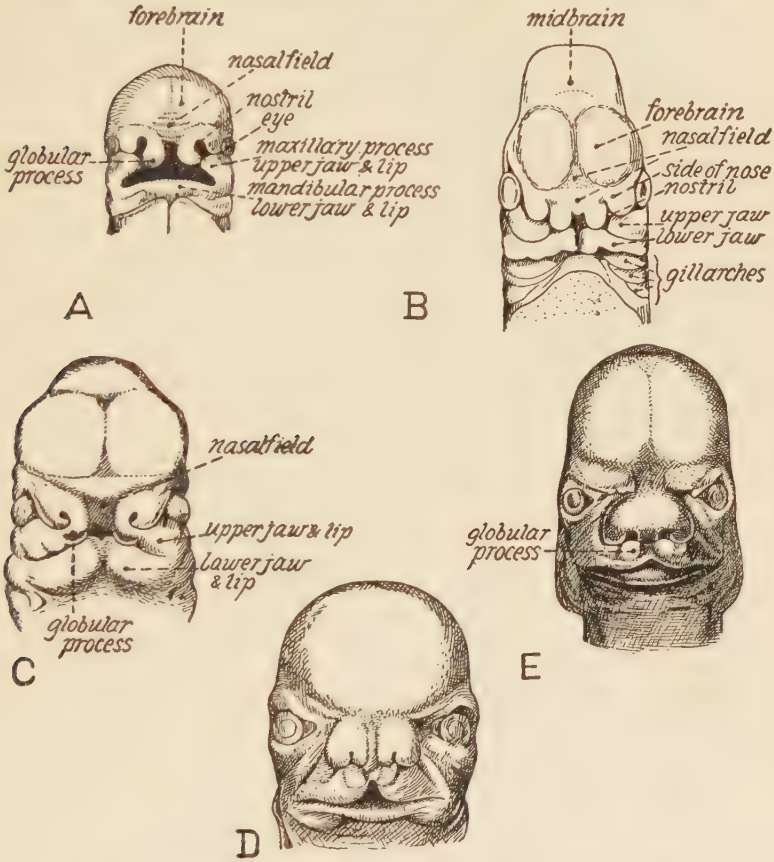

FIG. 86. EMBRYONIC DEVELOPMENT OF THE FACE IN MAN. (FROM EIDMANN, A, B, AFTER HIS, C, AFTER RABL, D, E, AFTER RETZIUS).
(From *Entw. d. Zähne . . .*, Hermann Meusser, Berlin.)
For details, see p. xxxiv.

important factors in producing the excessively different extremes shown in Fig. 89.

Let us consider further then the general course of embryonic development of the nose. In all mammals, including man and the anthropoid apes, the face in front of the eyes is formed during individual development (Fig. 86) by the growing

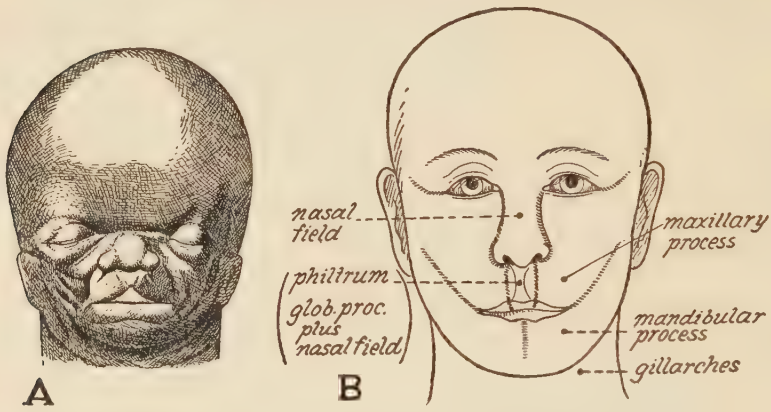

Fig. 87. Fœtal (A) and Adult (B) Development of the Face in Man. (A, from Eidman, after Retzius; B, Modified from Keith).

(A, from *Entw. d. Zähne . . .*, Hermann Meusser, Berlin.)

For details, see p. xxxiv.

together in the mid-line of a system of five flaps or rounded processes, four of which represent the opposite halves of the cheeks and upper and lower lips and jaws, while the fifth, a median area (the nasal field) forms the middle of the philtrum of the upper lip and the middle part of the nose. The sides of the nose are formed from the growing together in the mid-line of the nasal field and the

enlarged olfactory capsules. The lateral or alar cartilages of the external nose represent a forward growth of the margins of the olfactory capsules.

According to Broom, the median cartilage or septum of the nose appears to have been derived originally from a forward prolongation of the base of the skull (presphenoid) and in the mammal-like reptiles, marsupials and some other orders of mammals it is still formed that way; but in man and other primates the forepart of the septum acquires a separate center of ossification and becomes the mesethmoid bone.

Schultz has shown (Fig. 88) that as development proceeds the middle cartilage (septum) grows forward and downward faster in man than in the anthropoids and faster in the white race than in the negro race; thus in the latter the everted lips and more protruding front teeth are associated with a less deep median septum and a lesser downgrowth of the nasal tip. In adults of all races the nose gets longer, narrower at the base and more raised at the bridge. Thus babies and young children have relatively shorter, less prominent noses than adults (Fig. 87).

The median partition (septum) that supports

the tip of the nose is tied to the bone above the incisor teeth. If then the front upper jaw bone

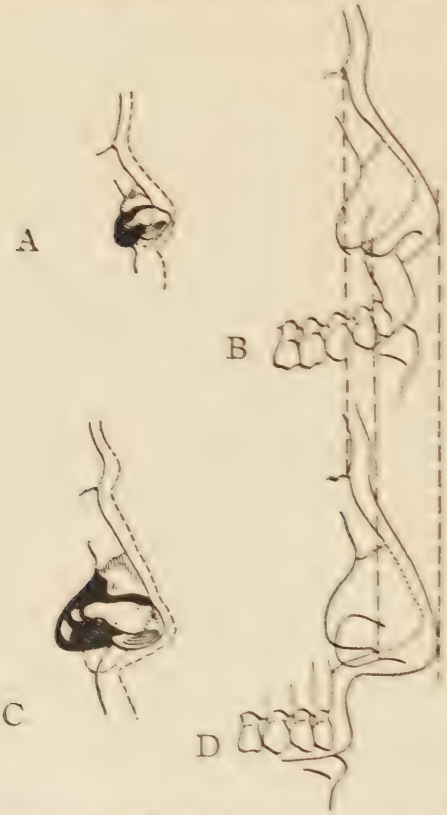

Fig. 88. Nasal Profiles and Related Parts in Man. A, Negro Child; B, Negro Adult; C, White Child; D, White Adult. (All after Schultz.)

For details, see pp. xxxiv, xxxv.

(premaxilla) has a feeble growth, it will not grow far forward (as it does in the anthropoids) and hence the anchorage of the median septum will be

relatively far back. This will tend both to increase the prominence of the nose as a whole and to give a downward inclination to the tip. In the typical Dinaric or Hittite nose (Fig. 89C) the resultants of all the horizontal, forward components and of all the downward components are very conspicuous.

If the transverse growth components of the palate are relatively weak, the bony palate may buckle up and the median septum may either bend on one side, producing a partial closure of the nasal passage, or possibly it may be displaced upward, producing a high-ridged or humped nose. If the bridge and the lower end of the nose as well as the median partition are all retarded in their growth, as in achondroplastic dwarfs, a marked repoussé or pug nose, with almost upturned tip, will result (see below, page 230). In the orang the median partition itself seems to lag in growth, while the orbits are crowded together and the nasal bones are extremely reduced.

The transverse components of growth are obviously in the ascendant in extremely wide noses with broad nostrils and low bridges, as in Australian and Tasmanian aborigines, Papuans, Melanesians, negritos and negros. Such conditions are apt to be associated with prognathous

jaws and large teeth (Fig. 89D). The reduction in size of the tooth row as a whole seems to have permitted or favored the vertical and forward growth of the nose, while the opposite tendency culminates in the gorilla, which has enormous teeth and an extremely broad nose. Doubtless other factors complicate the results, for instance, the lateral cartilages or alæ of the nose must in themselves have varying growth power, very feeble in the orang, vigorous in the gorilla, still more so in man.

The form of the nose bridge is likewise conditioned by many factors. The greater the volume of the brain in the fœtus, the sharper will be the bending of the brain upon itself, and the further forward will be pushed the greater wings of the sphenoid bone and the temporal region of the skull. All this has a tendency to push the face forward, especially the lateral angles of it, so that in extremely wide-headed forms the cheeks often protrude and the outer corners of the eye-orbits are far forward. This produces the Mongolian type of broad flat face, often with a wide space between the orbits and a low flat bridge and protruding eyes. The varying shape of the lower end of Mongolian noses is perhaps correlated with

Fig. 89. Extremes of Nose Form in Man: (A) African Pygmy; (B) Tyrolese; (C) Armenian; (D) South African Bushman. (A, B, from Martin, after Czekanowski, D, after Schultz; C, after von Luschan).

(A, B, D, from *Lehrbuch der Anthropologie*. Gustav Fischer).

For details see p. xxxv.

other factors, such as the width of the palate.

Among other possible factors affecting the shape of the nose is the extent of upward growth of the frontal process of the superior maxillary bone (Fig. 50). This process is a small prong or fork, one on each side of the head, in contact with the frontal above and supporting the nasal bone. An increase in size of this process would tend to elevate the bridge of the nose. Similarly a down growth of the whole maxillary bone, as in acromegalic persons, produces a marked vertical lengthening of the nose.

Here we touch upon the question, what causes all these individual growth differences? The cretins and achondroplastic dwarfs, which have broad pug noses, have deficient thyroid glands, and the acromegalics with very long noses and protruding chins have diseased pituitary glands. For these and other reasons many authors are inclined to look upon the "hormones" that are thrown into the blood stream by the different endocrine glands as stimulators of differential growth or development; but it is also recognized that each growing part has its normal range of response or receptivity to the appropriate hormones. Con-

sequently the mechanism of the development of any given part may be threefold: that is, it may involve first, its own inherent and probably hereditary growth power; secondly, the quality or amount of specific hormones produced by the endocrine glands; thirdly, the degree of receptivity of each part to the stimulation of the hormones.

The common saying, "As plain as the nose on one's face" is an unscientific recognition of the dominance of the nose in the human physiognomy. The studies of Schultz on the development and growth of the human nose, and of Stockard on the principles and factors of development and growth in general give us a slight hint of the complexity of the factors that mould the individual nose. Except in the case of identical twins no two persons will carry the same hereditary factors affecting nose form, while even in the case of identical twins the nutritional factors can hardly be exactly the same, especially after birth. The resulting diversity in nose form is as bewildering as the diversity in patterns of a kaleidoscope and, at least to some extent, is conditioned by the same law of chance associations of hereditary and environmental influences.

Fig. 90. Extremes in Face Form and Color: (A) Hottentot Woman (from Martin, after Poech, *Lehrbuch der Anthropologie*, Gustav Fischer); (B) Nordic Swede (from Lundborg and Runnström, *The Swedish Nation*, H. W. Tullberg.).

OUR BEST FEATURES

Optical Photography and its Results

THE HUMAN EYES AS INSTRUMENTS OF PRECISION

All sense organs are instruments of precision that register varying intensities of the pulsing streams of energy to which they are exposed. The paired eyes of man, together with their connections in the central nervous system, register even slight changes in the intensity of light, they respond to a wide range of its wave length, and hence discriminate colors, and they are extremely sensitive to the movement of images across the retina. Through their binocular adjustments they record extension, relative distances, and movements in a three-dimensional field, and by their biconjugate movements they can find a moving image and keep it in focus within wide limits.

THE EYES OF INVERTEBRATES

The anatomy and physiology of the eyes of invertebrates and vertebrates are the subjects of an enormous literature, which has been admirably summarized by L. Plate in his *Allgemeine Zoologie und Abstammungslehre*, Zweiter Teil, Jena, 1924, wherein are set forth more fully most

of the facts cited in the present chapter.[1] The lower forms of animals exhibit a wide diversity of organs sensitive to light, in various stages of complexity. Too long exposure to the ultra-violet rays has an injurious or even fatal effect on many organisms, such as bacteria, infusoria, hydroids, rotifers, nematodes, etc. (Plate, 1924, p. 386), which hence shrivel up or shrink away from these rays, while as everyone knows, plants turn toward the sunlight and some animals love to bask in the sun. Hence in view of the importance of light to the organism in one way or another, it is not surprising that even in very simple one-celled forms such as certain protista there should be clear granules, like lenses, sometimes backed by dense pigment, which may in some way act as rudimentary eyes and contribute to the organism's different reactions to light of different intensities (Plate, 1924, pp. 424–427). At any rate, when we come to certain of the jellyfishes we find undoubted eyes or ocelli in the outer layer or

[1] Professor Plate (*in litteris*) calls attention to the fact that, considering the enormous range of electric waves (from almost zero to hundreds of kilometers), it is remarkable that the whole gamut of human sensation of light, color, form and movement, with all their derived pleasures, is caused by so relatively narrow a range of electric waves. "How different our picture of the world would be," he writes, "if we had more such regions!"

ectoderm of the cup-shaped body. In some cases (Fig. 91A) each ocellus consists only of a slightly raised patch of larger pigment-bearing epithelial cells alternating with smaller "light cells." The patch grades into the ordinary epithelial cells around it. In other cases (Fig. 91B) the patch

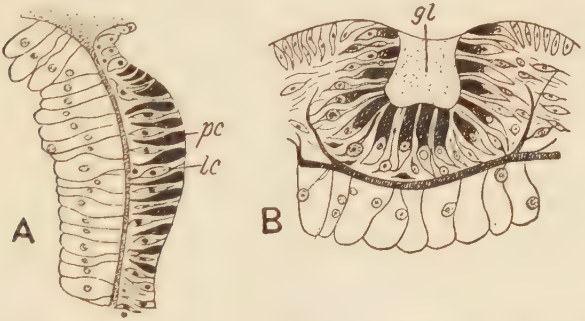

FIG. 91. THE BEGINNINGS OF EYES. (FROM PLATE, AFTER LINKO.)

A. Section of an ocellus, or eye spot, at the base of a tentacle of a jellyfish. B. Section of a "goblet eye" of a jellyfish.

(From *Allgem. Zool.*, Gustav Fischer.)

For details, see p. xxxv.

sinks below the surface, forming a pouch lined with pigment. Between the large deeply pigmented cells on the inside of the pouch are small "rods" at one end of the "light cells." Such an alternation of two kinds of cells foreshadows the alternation of the "rods" and "cones" of more advanced types of eyes, in which the "rods" are believed to detect light and darkness, form and

movements, while the "cones" chiefly detect color differences (Plate, 1924, p. 705). In the jellyfishes the cavity of the optic pouch is often filled with a transparent jelly-like substance corresponding to the "glass body" or vitreous humor of higher eyes, and functionally to the lens. That these organs are really eyes, says Plate (1924, p. 428), follows from the fact that if the animal is deprived of them it fails to react in its normal way to light.

In some of the flatworms the eyes consist of hollow capsules derived from an infolding of the epithelium and deeply lined with pigment. Each capsule has sunk beneath the epithelium, which has grown over it. It is open on one side and into its hollow interior project the flower-like ends of the "light cells," the outer ends of which pass into elongate nerve cells. Hesse (quoted by Plate, p. 433) notes that if two such capsules are symmetrically arranged on either side of the midline, then a light in front will give symmetrically placed shadows inside the capsules, a light on the left side will illuminate the left capsule and leave the interior of the right one in shadow, and so forth. Thus the nerves inside the capsules on

opposite sides of the body will be stimulated differently according to the direction of the light

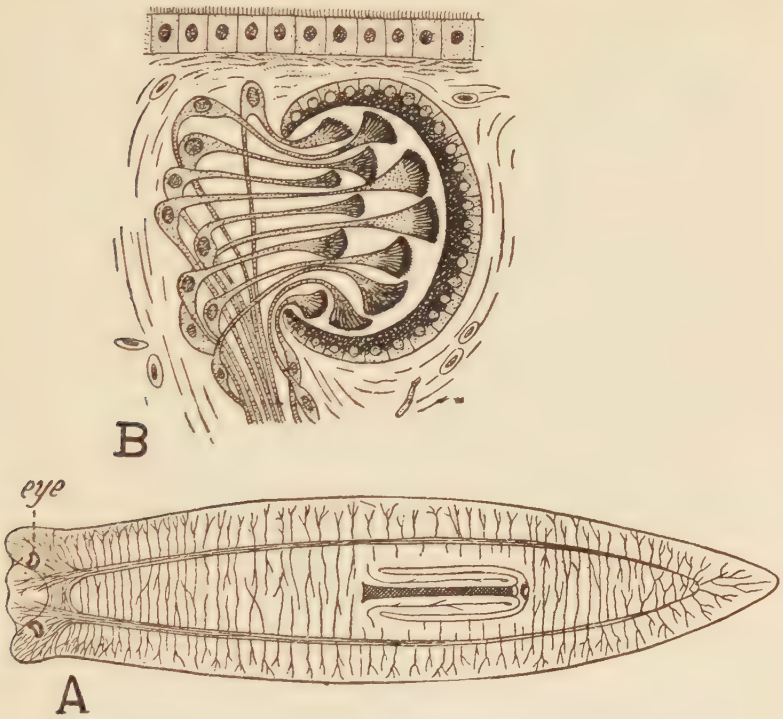

Fig. 92. Eye Capsules of Flatworm: (B) Section of "Goblet Eye" (from Plate after Hesse); (A) Location of Eyes (after Parker and Haswell).

(B, from *Allgem. Zool.*, Gustav Fischer.)

For details, see p. xxxv.

and according to their own orientation in the body. Here the function of paired eyes in enabling the organism to adjust its own axis of locomotion to the direction of the light comes into view.

Indeed, Plate (1924, pp. 738–742) cites much evidence for his view that *the paired eyes of vertebrates originated as directional organs, guiding the animal toward the light and that later by acquiring a lens they became true visual organs.*

Fig. 93. How the Eye Capsules of a Flatworm Serve as Directional Organs (from Plate, after Hesse).

The arrows show the varying directions of the light. In each case only a particular part of each retina is stimulated, the rest being in shadow.

(From *Allgem. Zool.*, Gustav Fischer.)

The higher invertebrates exhibit eyes in all grades of evolution, from the simple types described above to the compound eyes of crustaceans and insects and to the elaborately constructed paired eyes of the higher molluscs. Eyes occur in various parts of the body and sometimes in great numbers, as in certain deep-sea cephalopods. The common scallop (*Pecten*) has numerous eyes along the scalloped edge of the mantle. Thus in typical invertebrates the eyes are essentially derivatives of the skin and may occur almost anywhere on the

surface of the body, but in the vertebrates the paired eyes are essentially an outgrowth of a definite part of the forebrain, only the outer parts of the eye (including the lens and cornea) being contributed by the epithelium; although eventually

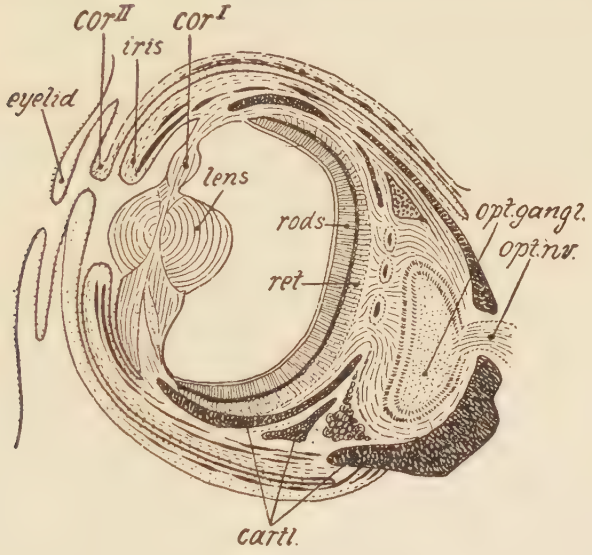

Fig. 94. Eye of Squid (Horizontal Median Section). (From Plate, after Hensen.)
(From *Allgem. Zool.*, Gustav Fischer.)

the brain itself has been derived from the same primary outer layer or ectoderm.

Among all the hosts of invertebrates the paired eyes which at first seem to approach the vertebrate type most nearly are found in some of the cephalopod molluscs, especially the squids and

octopuses. In these highly elaborate organs there are eyelids in front of the eyes, a contractile iris, muscles of accommodation, a highly complex retina of many layers, a large optic nerve and muscles to move the eyeball. But when we compare the parts of these cephalopod eyes with those of vertebrates we find many striking and profound differences. Thus in the squid (*Sepia*) the lids serve as a pupil, there are two corneas, the outer one perforated, the inner one dividing the lens into inner and outer parts; the so-called iris lies entirely outside of the retinal layer instead of next to it as in the vertebrates; and there is apparently no true choroid layer. More important still, in the cephalopods the optic nerve lies entirely behind the retina, while in vertebrates it pierces the retina and is then distributed over its front surface; finally, in the cephalopods the rods are on the front layer of the retina, pointing toward the light, while in the vertebrates they are on the back layer of the retina and point in the opposite direction.

Not all the cephalopods have eyes as complicated as the type described above and there is a gradation of forms leading back to the very

simple eye of *Nautilus* (Plate, 1924, pp. 474–478). The retina and indeed the whole eye of cephalopods develops in the embryo as a pouch in the skin, and is thus comparable only to the lens of vertebrates; in the latter the retina is developed from the optic

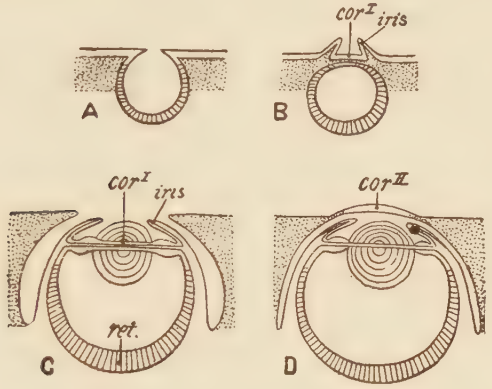

Fig. 95. Development of the Eye in Cephalopod Molluscs. (After Plate.)
(From *Allgem. Zool.*, Gustav Fischer.)
For details, see p. xxxvi.

cup, which is an outgrowth of the brain. Thus at every important anatomical point the paired eyes of cephalopods and of vetebrates differ profoundly from each other. From all this it is evident that the paired eyes of cephalopods and of vertebrates are not homologous with each other at all, that they have arisen from dissimilar beginnings and have come to resemble each other

by convergent evolution in adaptation to similar functional needs.

The paired eyes of the modern *Limulus* and the scorpions represent specialized offshoots of the annelid and primitive crustacean types (Plate, 1924, pp. 537–561). Patten and others have attempted to show how they might have been tranformed into the vertebrate eyes, but most authorities consider that there is no direct evidence in favor of this view and the profound differences between the eyes of arthropods and those of vertebrates have always been considered a grave objection to Patten's theory of the origin of the vertebrates from arthropods related to the eurypterids and to *Limulus*.

ORIGIN OF THE PAIRED EYES OF VERTEBRATES

We have seen above that a comparative study of the eyes of invertebrates shows several steps in the evolution of such elaborately constructed paired eyes as those of the cephalopods and therefore gives us a general idea how the somewhat similar paired eyes of vertebrates may have been produced. More direct evidence as to the origin of the vertebrate eye is wanting. The lancelet

Amphioxus, which, as all beginners in zoology learn, supplies us with an ideally simplified chordate, goes too far for our present purpose in the simplification of its eyes, which have either vanished entirely by degeneration or never developed.

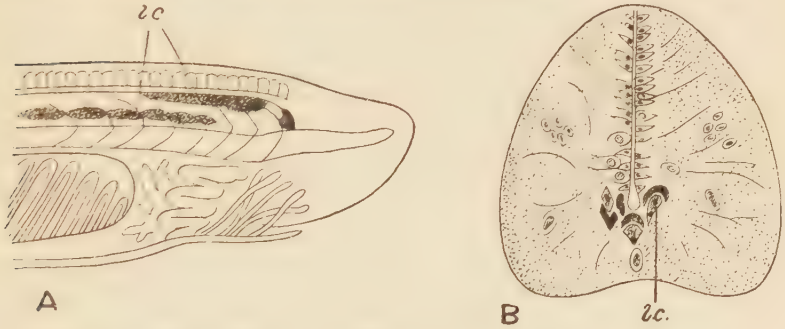

Fig. 96. Light Cells of Amphioxus: (A) Forepart of a Young *Amphioxus*, Enlarged; (B) Cross-section of the Spinal Cord of Amphioxus (from Plate, A, after Joseph, B, after Hesse.)
(From *Allgem. Zool.*, Gustav Fischer.)
For details, see p. xxxvi.

According to Plate (1924, p. 494) the lancelet (*Amphioxus*) when resting on the sandy bottom is supposed to sense the direction of the light by means of long rows of minute eye-like organs, which are deeply buried in the spinal cord and extend along each side of the back above the notochord. Each little eye consists of a single cell, supposed to be sensitive to light, backed by another cell which is concave and deeply pigmented. A much larger spot of pigment at the

front end of the brain tube is interpreted by Plate (1924, p. 493) not as an eye at all, as it lacks light cells, but as the last remnant of a balancing organ. Thus the light-sensing apparatus of *Amphioxus* is of the utmost simplicity and has little obvious relation to the highly complex paired eyes of vertebrates.

In the foregoing pages we have reviewed the general construction of paired eyes, we have outlined the evolution of eyes from very simple beginnings, we have considered the wide contrast between vertebrates and invertebrates in the structure of the paired eyes and we have seen that according to present evidence the vertebrate paired eyes do not appear to be inherited from any of the more complex invertebrate types but seem to have arisen in the very ancient and still undiscovered pre-vertebrates. As direct evidence from successive fossil stages illustrating the origin of the paired eyes of vertebrates is meager or wanting and as there are apparently no surviving pre-vertebrate stages except possibly *Amphioxus*, we must rely chiefly upon the evidence afforded by embryology, and such evidence is often open to the suspicion that we may be mistakenly inter-

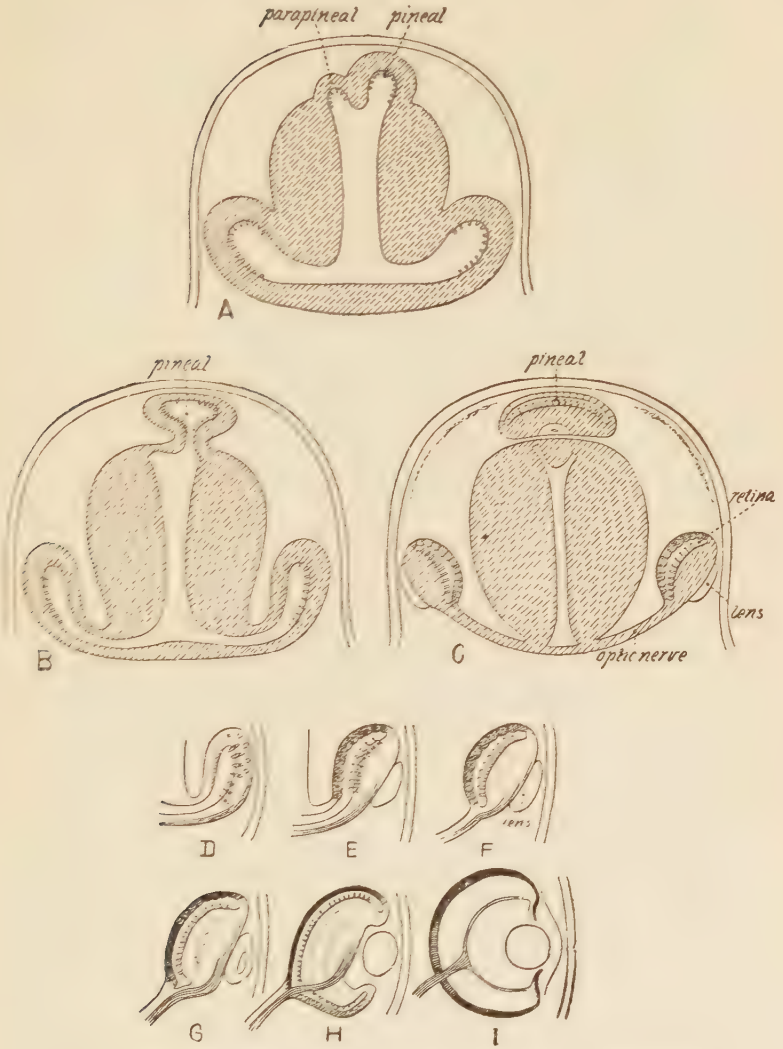

Fig. 97. Evolution of the Vertebrate Eye as Conceived by Studnicka (from Plate, after Studnicka).

(From *Allgem. Zool.*, Gustav Fischer.)

For details, see pp. xxxvi, xxxvii.

preting as a repetition of long past adult stages such arrangements or conditions as may be merely adaptations of the growing embryo to its own physiological needs.

Studnicka (quoted by Plate), basing his theory chiefly on the embryology of the lampreys and their relatives (which may represent the degenerate descendants of the ostracoderms), holds that originally there were two pairs of paired eyes in the pre-chordates, one pair dorsal, on the top of the head, consisting of the pineal and parapineal organs, the second pair low down on the sides of the head, the eyes of later vertebrates. Both pairs were derived from patches of cells sensitive to light, located in the broad sensitive tract that later folded up to become the brain tube. Up to this time both sets of eyes had served merely to orientate the animal with reference to the direction of light. When as a result of its growing mass the primitive nerve tract swelled outward, its crests grew upward and curved over toward the mid-line, carrying the primary optic depressions on to its inner side, so that the future "rods" would now point away from the light, and their nerve fibers, formerly beneath them, would now be bent

around toward the outer surface. Meanwhile the dorsal pair near the front edge of the brain tract were not turned over, so that their retina remained on the outer side of their nerve layer. As the brain swelling increased it pressed the future optic cups against the epithelium on the surface of the head; the epithelium sank inward, folded up into a lens, and the lens in turn increasing rapidly, conditioned the insinking of the optic swelling, which thus became the optic cup. The optic stalk or nerve is simply the constricted part between the brain and the cup. By this time the lateral paired eyes were becoming true organs of vision, while the dorsal pair gradually degenerated and their nerve stalks finally became the pineal and parapineal organs of the brain. It is important to remember that the retina apparently represents an inverted patch of epithelium and that the layer of nerve fibrils now covering it represents the former underside of the patch. Also that the optic cup was pushed in from the outside so that its primary cavity was squeezed out of existence.

The lens is at first connected with its parent epithelium by a slender stalk, which is soon lost. The lens thus finds itself protruding into the hollow side of

the pushed-in ball, or optic cup. The space between the lens and the inside of the cup becomes filled with fibrillar tissue which gives rise to the transparent jelly-like substance called the vitreous humor.

The retina, derived from the inner layer of the cup, comprises the following series of layers: the innermost of these is a layer of nerve fibers and ganglion cells which are gathered together and pierce the center of the cup, issuing from it as the optic nerve; next follow various layers of large and smaller nerve cells, culminating in the layer of cones and rods, the latter being nearest the outer epithelial layer of the inner wall and directed away from the source of light. The outer layer of the optic cup gives rise to the pigmented layer of the retina, which doubtless provides the necessary opaque, light-proof layer, like the black inner surface of a camera. Next comes the network of blood vessels of the choroid, while outside of the choroid is the thick sclerotic layer, which is continuous in front with the cornea.

ORIGIN OF THE HUMAN EYES

Before attempting to trace the evolution of the human eye, let us recall its broader structural

features. We know that it is essentially like a camera, with its dark chamber (the inside of the eyeball), its lens, its sensitive plate (retina), its iris-diaphragm for regulating the amount of light admitted through the pupil. We know also that it differs from an ordinary camera in altering the focus not by regulating the distance between the lens and the plate but by changing the curvature of the elastic lens through the pull of the ciliary muscles. We also know that the human eye differs from a single camera in being linked with its fellow of the opposite side so as to provide for a binocular, stereoscopic mental image and that the two eyes are biconjugate, that is, by means of its six eye muscles (Fig. 98), each eye can move in harmony with its fellow so as to keep a moving object in focus; also that the eye is a living mechanism provided with elaborate systems for the elimination of waste, for automatic renewal of all parts and for the lubrication, cleaning and protection of its exposed surface.

The retina carries a coloring matter named rhodopsin or visual purple,[1] which becomes rapidly bleached on exposure to sunlight. No doubt the

[1] Cunningham, D. J., 1902, *Textbook of Anatomy*, p. 689.

extent and intensity of the bleaching effect is in some way proportional to the size of the aperture, the intensity of the light and the length of exposure. And no doubt also the innumerable rods and

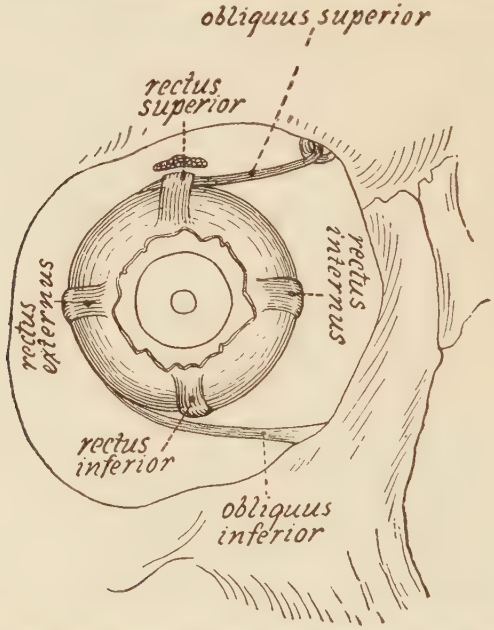

Fig. 98. The Right Eyeball and Its Six Muscles (from Plate, after Merkel and Kallins).
(From *Allgem. Zool.*, Gustav Fischer.)

cones of the visual field react differently to different wave lengths (colors) and different intensities (light and shade), so that an image made up of innumerable points, like a half-tone picture, is recorded on the retina. But whereas the photographer proceeds after an interval to fix the image

on the plate, the retina immediately proceeds to "televisualize" its images through the myriads of nerve fibers covering its surface. After passing through many microscopic relay and "booster" stations the disturbances pass along a vast cable route known as the optic nerve. Instantly reaching their first main destination, the visual cortex of the brain, the visual currents now incite millions of repercussions which are flashed and reflashed to the relay stations and great central systems in many parts of the brain, where they set off many triggers that control the secretory activities of glands or the contractility of muscle fibers.

The foregoing description holds in a general way for the eye of vertebrates of all grades from fish to man, the vertebrate eye, except in degenerate forms, being extraordinarily constant in its main features. Hence the basic features of the human eye date back to the beginnings of the vertebrates and are fully exemplified in such primitive forms as the sharks (Fig. 99). The six eye muscles of the human eye (Fig. 98) likewise date back at least to the shark-like stage. Here again the shark is vastly nearer to man in the essential features of its

morphology than it is to any known invertebrate. In other words, while we can only surmise what the history of the eye may have been below the vertebrate stage, we have the most convincing evidence that once that grade of organization of the eye had

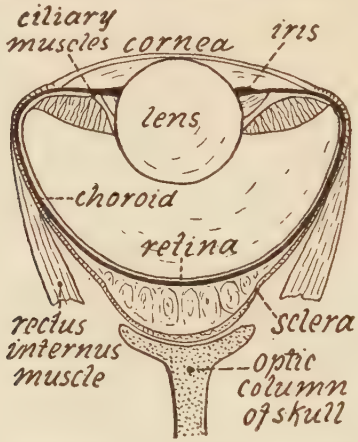

FIG. 99. THE RIGHT EYE OF A SHARK IN HORIZONTAL SECTION (FROM PLATE, AFTER FRANZ).
(From *Allgem. Zool.*, Gustav Fischer.)

been attained, it was transmitted by heredity with only minor improvements from fish to man.

Although the human eye is undoubtedly derived remotely from one that was in general like the shark type (Fig. 99), from which it has inherited even the principal layers of the retina, it shows also many progressive changes beyond that of the shark in adaptation to vision in the air rather than in water. Its lens, being relatively smaller and

flatter than that of the shark, gives a longer focus, and accordingly the focal axis of the bulb is lengthened, the human bulb being spherical while that of the shark is flatter in front. The cornea in

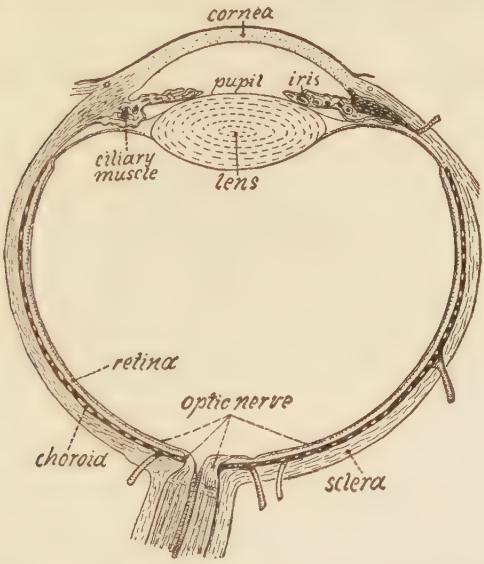

Fig. 100. Diagram of Horizontal Section of the Right Human Eye (Simplified from Plate, after Luciani).

(From *Allgem. Zool.*, Gustav Fischer.)

man is more convex and widely separated from the lens, which is entirely behind the iris, whereas in many sharks it protrudes through the pupil and touches the cornea. The human lens is much more delicate, less dense, more easily compressible than that of the shark and it readily responds to the pull of the ciliary muscles of accommodation.

As to the external accessories of vision, man retains a vestige of the nictitating membrane or third eyelid of lower vertebrates in his semilunar fold at the inner corner of the eyelid; but he has advanced far beyond the shark in possessing an elaborate lacrymal or lubricating apparatus, con-

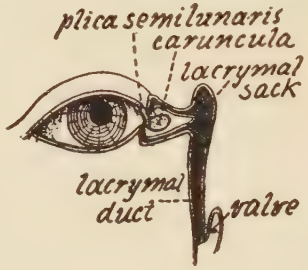

Fig. 101. Tear-draining Canals of the Eye (after Keith).

sisting of tear-producing glands, with two collecting canals above and below the caruncula. These two canals converge toward and drain into the lacrymal sac, which is lodged in a pocket of the lacrymal bone on the inner wall of the orbit; the lacrymal sac is continued downward through the naso-lacrymal duct into the nasal chamber. Man also has fleshy, movable eyelids, which are provided with eyelashes and Meibomian glands.

Many similar details could be cited in which the human eye is superior to that of the shark; but

the anti-evolutionist could find little justification for setting man apart from the rest of creation on this account, for we find that every one of the characters cited above is the common property of normal land-living mammals and that the evolution of some of these structures, such as the lacrymal apparatus and the third eyelid, can be traced with convincing detail through the various branches of the vertebrate tree lying between the human and the shark branches.

Moreover we are compelled to cause even further distress to the indomitable critics of the Darwinian theory of human origin by bringing forward again their special horror, the anthropoid apes and monkeys. For nowhere will more convincing morphological evidence of the relatively very close relationship of man to these animals be found than in a detailed comparison of the anatomy and physiology of the paired eyes. And when to these resemblances in the visual organs between man and anthropoid, we add the striking identity in the complex arrangements and connections of the optic tracts within the brain, as reported by the leading students of the human and anthropoid brains, the evidence for Darwin is heaped still higher.

The position of the eyes in the human head has likewise been inherited from the common man-anthropoid stock. In *Notharctus*, a primitive primate of the Eocene epoch (Fig. 35A) the eyes were directed partly outward as well as forward, the large muzzle extended far in front of the orbits and binocular vision was obviously impossible. The large size of the olfactory chamber in *Notharctus* also indicates that like other mammals and especially like its relatives the modern lemurs, the lowest existing primates, it still depended largely upon its olfactory sense, while the higher primates have a much reduced olfactory apparatus and a predominant visual apparatus. With regard to the direction of the orbital axes, these look partly outward also in most of the modern lemuroids (Fig. 35B) and even the greatly enlarged orbits of the modern *Tarsius* (Fig. 35C) are directed somewhat away from each other. In the South American monkeys (Fig. 35D) however, the outer angles of the orbits are shifted further forward and the muzzle is reduced; in the Old World monkeys and anthropoid apes (Fig. 35E, F), this process is completed and binocular vision is established. The binocular character of the vision of anthropoids and

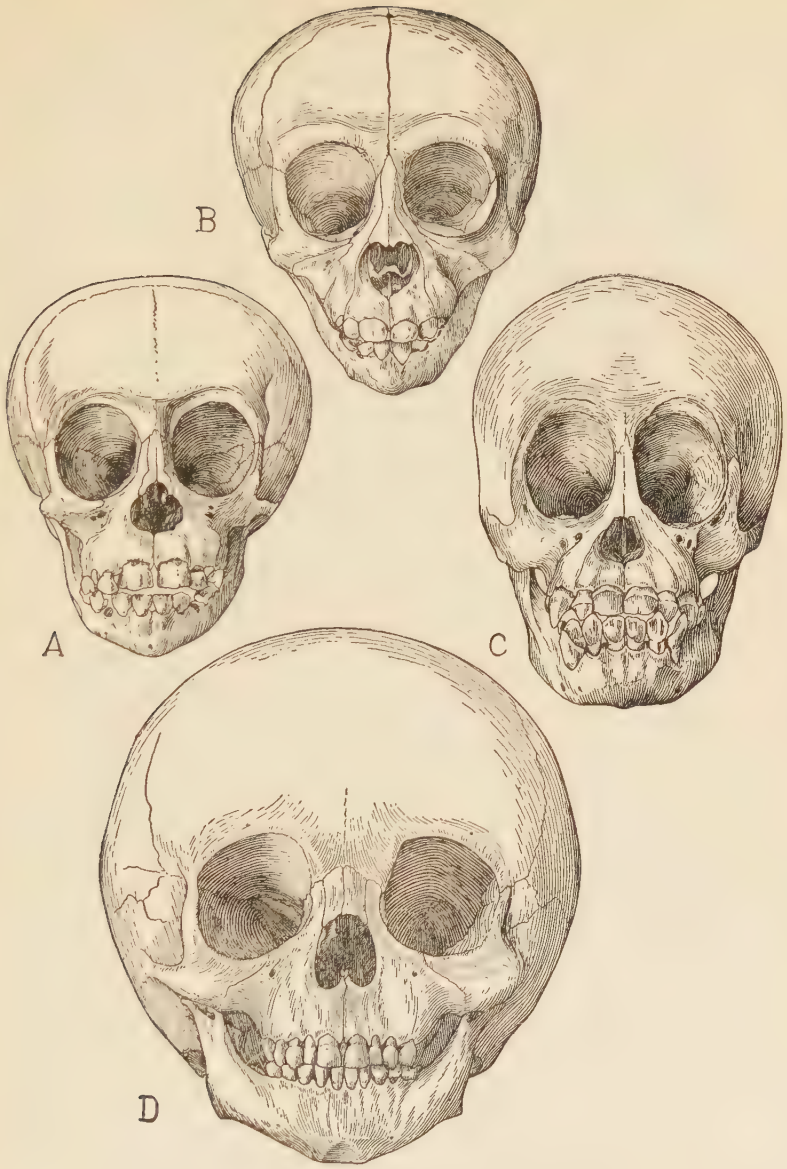

Fig. 102. Front View of Infant and Young Skulls of Anthropoids (A, B, C) and of Man (D).

For details, see p. xxxvii.

man is especially evident in the front views of the young skulls (Fig. 102).

Meanwhile we observe a general progression in the character of the hands, which in the lemuroids are hardly more than forefeet, while in the gibbon, chimpanzee and gorilla the anterior extremities are true hands, adapted primarily for brachiation or leaping with the arms, a habit which requires the greatest quickness in adjusting the focus of the eyes and in correlating the locomotor activities with the rapidly changing visual data.

To the brachiating habit of his ancestors man doubtless owes much of his skill in discriminating the relative nearness of different objects. Brachiation would also seem to be greatly facilitated by biconjugate movements of the eyes. Broman and John I. Hunter have shown that in the chimpanzee the nucleus in the brain of the oculomotor nerves, which controls several of the eye muscles, has essentially the same pattern as in man and differs widely from that of the lower primates which have not attained biconjugate movement of the eyes.

The surface of the iris as seen through an ophthalmoscope differs widely in different kinds of animals. Lindsay-Johnson in his beautiful

monograph on the fundus oculi of vertebrates figures the retinal surface of the eye of many mammals, including a white man, a negro and a chimpanzee. The deeply pigmented iris of the chimpanzee shows the most striking resemblance to that of the negro, while its basic similarity to that of the white man is masked by the loss of pigment in the latter. Only man and the apes have a macroscopic "macula lutea" or spot of clearest vision on the retina (Plate, 1924, p. 690).

The lacrymal bone, in the inner corner of the eye, affords additional evidence of the close relationship of man and the anthropoids. Not only are its general form and connections strikingly similar in man and chimpanzee (save for the very small size of the "hamular process" in the apes) but Le Double notes[1] that in Deniker's gorilla fœtus the lacrymal bone begins to ossify in the same place that it does in the human fœtus toward the end of the fourth month, namely, in the covering membrane of the ethmoidal cartilage and on the inner side of the lacrymal sac; that, like the human fœtal lacrymal, it consists of an

[1] "Essai sur la Morphogénie et les Variations du Lacrymal et des Osselets péri-lacrymaux de l'Homme." *Bibliographie Anatomique*, 1900, T. VIII, p. 125.

oval plaque with its long diameter inclined obliquely from above downwards and from within outward. Le Double further notes[1] that during intrauterine life the human lacrymal is successively oval, triangular and quadrilateral in form, that the lacrymal of the gorilla is almost triangular, while those of the adult chimpanzee and orang, which show so much resemblance to the human lacrymal, are also subject to the same variations in form.

CONCLUSIONS

In conclusion, the human eyes owe their beginnings to the sensitivity of protoplasm both to the injurious and the beneficial effects of light. In their early pre-vertebrate stages they seem to have been merely directional organs to orientate the animal's locomotion with reference to the light, serving the same purpose at the lower sides of the head as the pineal and parapineal eyes did on the top of the head (Fig. 97A). At this stage the eyes were still on the inner side of the brain tube. When the brain grew outward into contact with the epithelium the optic cup acquired a lens

[1] Ibid., pp. 128, 129.

and true vision resulted, greatly enhancing the organism's success in the pursuit of living prey and in the escape from its enemies. Then various accessory organs appeared, for regulating the focus of the lens, either by slightly changing its position with reference to the opening, or by altering its curvature. After the air-breathing fishes crawled out of the swamps their eyes had to become accustomed to functioning in the air and we find further improvements in the accessory devices for accommodation and for protecting and keeping in repair the whole delicate apparatus. These devices culminate in the mammals, in which however for the most part the olfactory apparatus rather than the eyes is still the dominant sense organ. The primates, alone, show a progressive reduction of the olfactory sense and a concomitantly increasing importance of the eyes, which is further emphasized in the arboreal brachiating anthropoids. In man, a secondarily terrestrial offshoot of the primitive anthropoid stock, the eyes retain not only all the advantages won by the vertebrates in their earlier predatory career, but also all the improvements resulting from a prolonged course of very active life in the

trees. Starting with all this experience the eyes of the first true man not only cooperated with the hands, but filled the brain with memory pictures, and these, on the principle of conditioned reflexes, came to be associated in definite combinations with the memories of vocally produced sounds. *Thus man's eyes and ears, rather than his nose, provided him with the means of rising above the endless round of life known to his predecessors, of turning his observational powers upon himself, and eventually of foreseeing not only the immediate but also some of the distant effects of his own activities.*

Primitive Sound Recorders

The human organ of hearing (Fig. 103) consists of three main parts: (1) the *external ear*, for collecting the sound waves; (2) the *middle ear*, including the tympanic or drum-membrane and the tympanum or middle-ear chamber, the latter containing the three auditory ossicles, the office of which is to transmit the vibrations of the drum membrane to the inner ear; (3) the *inner ear*, or labyrinth, comprising (a) the three semicircular canals with their basal connecting chamber or utriculus, the canals and utriculus being concerned

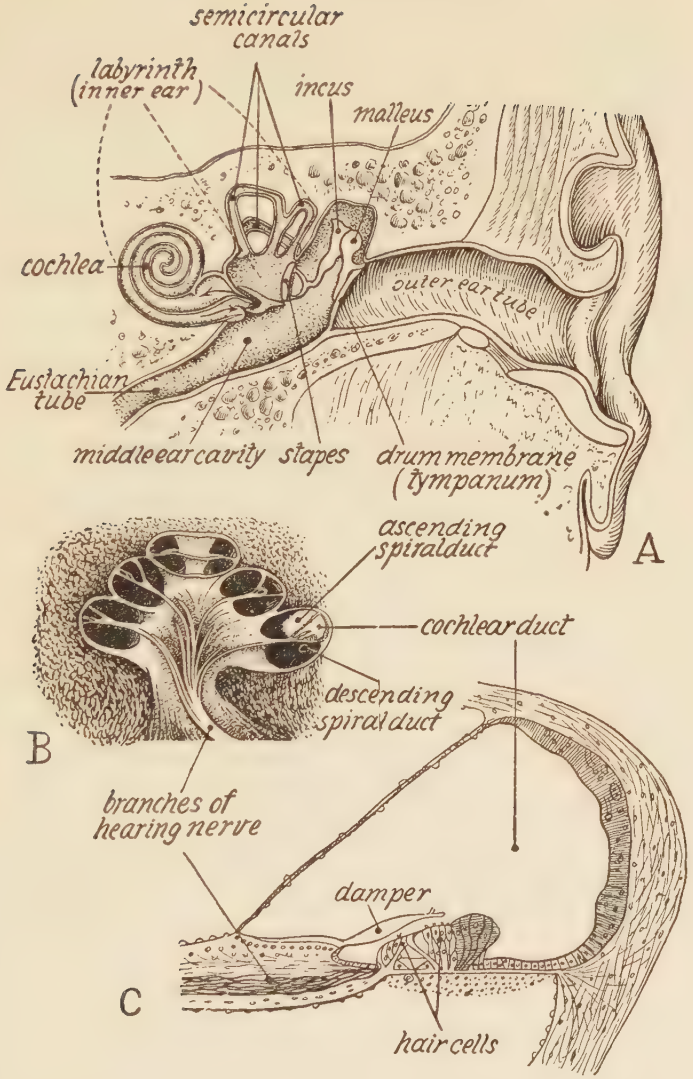

FIG. 103. THE HUMAN ORGAN OF HEARING AND BALANCE.

(A) Transverse section (after Cunningham); (B) Diagram section of the cochlea; (C) Greatly enlarged view of the cochlear duct.

[For details, see pp. xxxvii, xxxviii.

with the sense of balance; (b) the cochlea, a spirally-wound double tube filled with liquid and containing between the upper and lower inner tubes the spirally-wound organ of Corti, the true organ of hearing. The sound waves in the air cause the drum membrane to vibrate, the ossicles magnify the movement and set up mechanical waves in the liquid of the cochlea. It is these mechanical waves and not the sound waves themselves that are picked up by the little rods of the organ of Corti and transmitted to the nerves of hearing.

In the more primitive fishes at the lower end of the vertebrate series there is no middle ear and the inner ear consists chiefly of the semicircular canals, which may be followed throughout the series without a break from fish to man.

The labyrinth arises in the embryo shark, as in the embryo man, by the formation of a sac or pocket in the ectoderm or outer cell layer on either side of the tube that gives rise to the hind brain. The sac later becomes surrounded by cartilage which finally ossifies. The nerves of the semicircular canals appear to be part of the fore and aft series that innervates the "ampullæ" of the

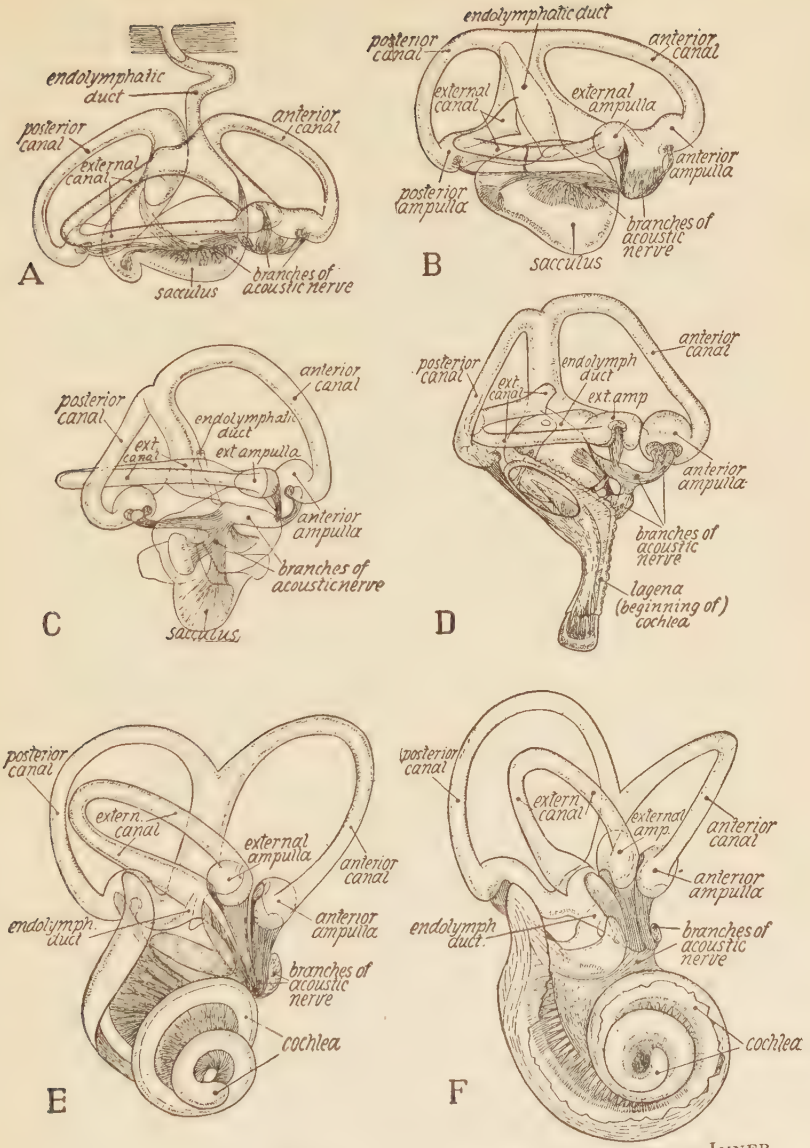

FIG. 104. SERIES SHOWING THE MEMBRANOUS LABYRINTH OR INNER EAR FROM FISH TO MAN. RIGHT SIDE; OUTER VIEW. (AFTER RETZIUS.)

A. Shark; B. Ganoid fish; C. Primitive reptile; D. Alligator; E. Rabbit; F. Man.

For details, see p. xxxviii.

shark (Fig. 6) and the lateral line organs in the skin of most fishes. These organs are sensitive to the disturbances caused in the water either by wind or by objects falling on the surface of the water (G. H. Parker). Below the semicircular canals there is a sac-like depression (Fig. 104A)

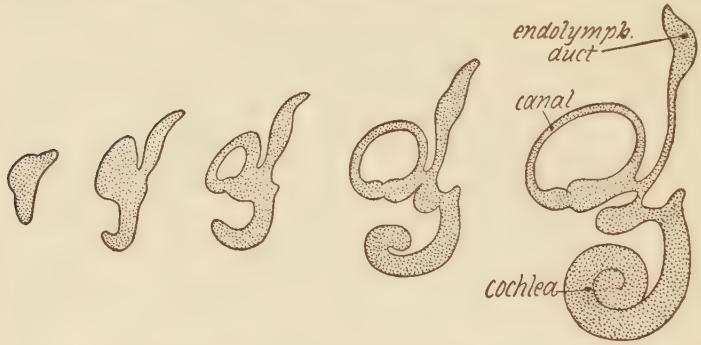

Fig. 105. Development of the Labyrinth or Inner Ear of Man (after Streeter).

frequently containing an otolith or calcareous secretion which may function in the sense of balance. The nerve that goes to the semicircular canals also sends off a branch which is attached to the otolith, and this lower branch, in the higher vertebrates, is the nerve of hearing (Fig. 104D–F).

It is doubtful whether fishes can really hear rather than feel sound waves in the water. The true organ of hearing equivalent to the cochlea of man has its inception apparently in the Amphibia

in the shape of two small papillæ which grow out from the side of the sac below the semicircular canals. In the crocodiles and alligators one of these papillæ is prolonged into a curved tube (Fig. 104D) and in the mammals (Fig. 104E, F) the tube is wound into a spiral, the cochlea. Thus while the semicircular canals which are concerned with balance show only minor changes as we pass through the long series from shark to man, the organ of hearing in air has its beginnings in the Amphibia and culminates in the typical mammals, from which it is transmitted intact to the apes and man.

The chamber of the middle ear (Fig. 106) in the frog (which represents a comparatively little-modified survivor of the earliest amphibians) is derived in the embryo from an out-pocketing from the throat, corresponding to the first or hyoid gill pouch of fishes. This chamber is therefore lined with the entoderm, or primary inner cell layer. The Eustachian tube of the frog is the short passage connecting the cavity of the middle ear with the cavity of the throat. By this arrangement the outward pressure of the air inside the mouth and throat neutralizes the inward pressure

of the air outside the ear-drum. Likewise in all higher vertebrates, including man, the cavity of the middle ear communicates with the throat through the Eustachian tube; this arises in the

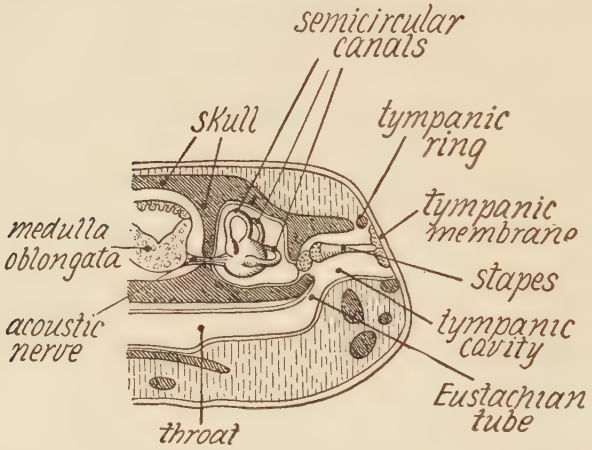

Fig. 106. Transverse Section of the Head in a Frog, Showing the Relations of the Middle Ear (there is no Outer Ear) to the Inner Ear and of the Latter to the Brain (after T. J. Parker and W. N. Parker).

embryo as an outgrowth of the primitive throat cavity immediately behind the first or jaw arch (Frazer, quoted by Keith).

The tube of the outer ear of mammals corresponds in position partly to the spiracle or hyoid gill cleft of the shark. Both arise also in the embryo as a down-pocketing of the ectoderm, which meets an out-pocketing from the throat

cavity called the hyoid gill pouch. In the sturgeon, a survivor of the primitive ganoids, W. K. Parker's plates of a very young embryo show the hyoid gill cleft lying in front of the upper part of the hyomandibula, or upper segment of the second gill arch. A spiracular cleft was also present in

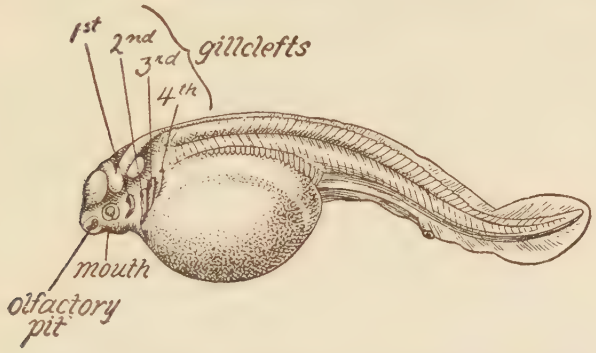

Fig. 107. Embryo Sturgeon, Showing Gill Clefts (after W. K. Parker).

the oldest fossil lobe-finned ganoid *Osteolepis* (Watson). In the earliest known amphibians and reptiles the spiracular cleft may be represented in part by the otic notch (Figs. 17, 19) upon which the tympanic membrane was stretched. In the fishes the gill chamber behind and below the spiracle was covered externally by the bony opercular flap, but in the oldest known amphibians this bony gill cover has disappeared, leaving the prominent otic notch open behind.

In the frog, a modern representative of the Amphibia, there is no external ear tube, since the tympanic membrane lies on the surface (Fig. 106). In the reptiles a ridge or fold of skin may guard the drum membrane and in the birds and typical mammals the latter has sunk so far below the surface that a deep tube is formed.

That the mammalian outer ear tube corresponds only at most in part with the spiracular pocket of the shark is indicated by the fact that the outer ear tube of mammals is formed below the Eustachian tube (which represents the lower part of the first internal gill pouch), while in fishes the spiracular pocket is formed from the upper part of the spiracular cleft and lies above the first internal gill pouch.

In *Echidna*, one of the egg-laying mammals, G. Ruge found that the cartilage of the external ear was continuous with the hyoid, or second gill arch, and hence the inference was drawn that the external ear cartilage was derived from the hyoid arch. But Gaupp's figures of the embryo *Echidna* show the hyoid cartilage entirely distinct from the external ear. And the relations of the ear tube to the tympanic ring both in *Echidna* and in other

mammals indicate that its cartilage is a new local development in the mammals.

The outer ear in mammals takes on a great diversity of forms, from the trumpet-like ear of antelopes and other keen-eared, defenceless herbivores to the huge and imposing ear-flaps of the

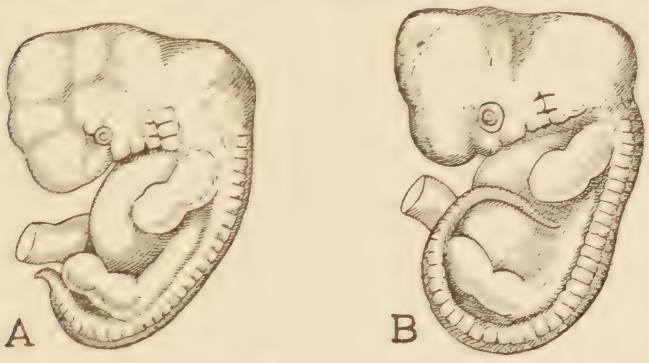

FIG. 108. HUMAN (A) AND MACAQUE (B) EMBRYOS, SHOWING ORIGIN OF THE EXTERNAL EAR FROM SIX TUBERCLES. (FROM LECHE, A, AFTER SELENKA, B, AFTER HIS, KEIBEL.)
(From *Der Mensch*, Gustav Fischer.)

African elephant. Some of the bats have large ears of extreme complexity, while the whales have only a thread-like tube beneath the skin that marks the last vestige of the external ears. Very little in detail is known either about the precise functioning of the different forms of external ear or about the origin and significance of its many subdivisions, such as the tragus, antitragus, crus of the helix and antihelix and the marginal fold or

descending helix and lobule. According to Keith (1921) in the human embryo of the sixth week all but the marginal fold arise from six tubercles that form around the first gill cleft depression.

> Three of these tubercles [writes Keith] grow from the mandibular or first arch and form the tragus, crus of the helix, and helix; three from the hyoid arch to form the lobule, antitragus and antihelix. The hinder margin of the ear, or descending helix, with the lobule, arise as a mere thickening or elevation of the skin behind the tubercles in the hyoid arch. Later in development the tubercles of the helix and antihelix send out processes which cross the upper part of the cleft and obliterate it, while the neighboring tubercles fuse to form the definite parts of the ear. The posterior margin and lobule rise up at the same time as a free fold.

Fig. 109. Ears of Fœtal Macaque (A) and of a Six Months Human Fœtus (B). (From Plate, after Schwalbe.)
(From *Allgem. Zool.*, Gustav Fischer.)

The common lemur (*Lemur catta*) of Madagascar has very large pointed ears that can be directed forward. In the monkeys the ear tends to be flat with a rounded top, quite different from the trumpet-like ear and not capable of being thrust far forward. The ear of the Old

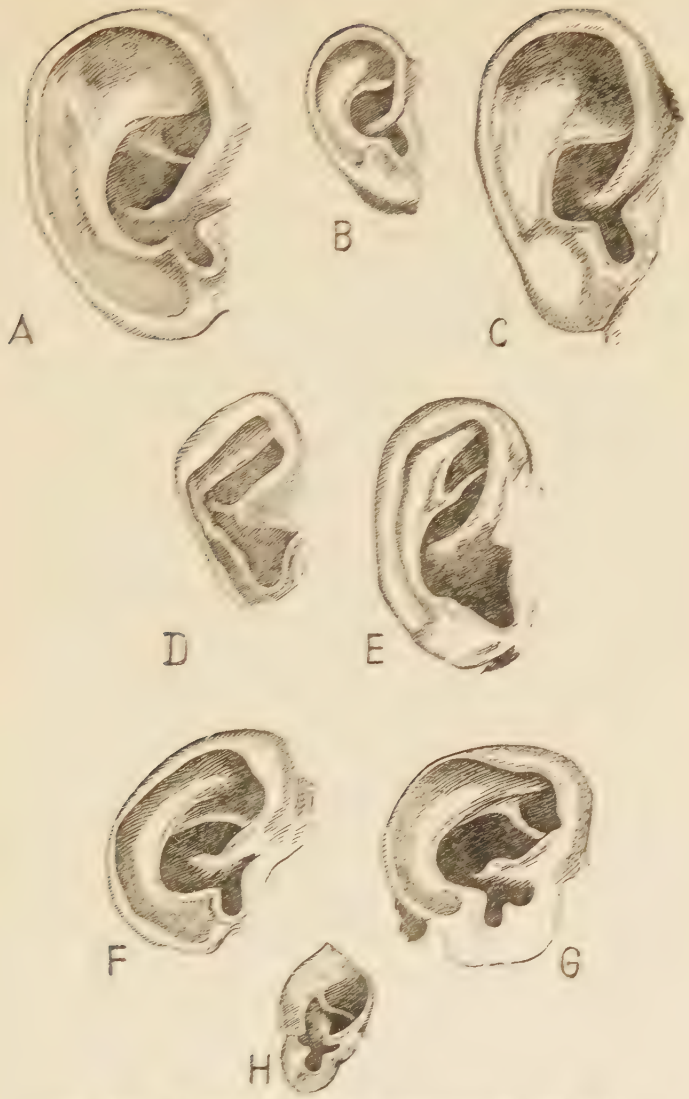

FIG. 110. EXTERNAL EARS OF ANTHROPOIDS AND MEN.
(AFTER KEITH.)

A. Chimpanzee. B. "Small chimpanzee type" (human). C. "Chimpanzee type" (human). D. Orang. E. "Orang type" (human). F. Gorilla; G. Gibbon; H. Lemuroid (Nycticebus).

World or catarrhine monkeys shows various stages in the reduction of the pointed tip (*cf.* Pocock, 1925, Fig. 36). The ear of a six-months' human fœtus (Fig. 109B) figured by Schwalbe has a truncate upper rim and vestigial tip and in general appearance approaches the Old World monkey type (Fig. 109A) as noted by Schwalbe. The unrolled outer rim and Darwin's point, found as an occasional variant in man, is reminiscent rather of the monkeys than of the anthropoids, although indications of the Darwin's point are not lacking in certain chimpanzees (*cf.* Hæckel, 1903, Pl. 26) and in certain orangs (Pocock, 1925, Fig. 37D, E).

The ears of the great anthropoid apes, while highly variable in details, are substantially of the human type, especially those of the gorilla. All have the rolled-over upper rim, but in the chimpanzee the hinder rim, according to Pocock (1925) is "sometimes flat, sometimes slightly overfolded but never apparently so overfolded as is typically the case in *Homo*. The lower lobe, varying in size, is not so well developed as in Man." On the whole the external ears of the gorilla and chimpanzee are remarkably human in appearance and, like so many other features of anthropoid anatomy,

they are literally one of the earmarks of man's relatively close relationship to the primitive brachiating ancestors of the chimpanzee-gorilla stock. If man had been derived from some entirely different stock of Primates there is no assignable reason why he should resemble the gorilla and the chimpanzee in so many external and internal characters in spite of his widely different habits and notwithstanding the millions of years that have passed since the human and gorilla-chimpanzee groups began to separate.

Since the time of Darwin the reduced ear muscles of man have been justly famous as indications of our derivation from mammals with more movable ears. Ruge's monograph (1887, Plates V, VI, VII) on the facial musculature shows very clearly the striking resemblance between the ear muscles of the chimpanzee and those of certain human embryos and children (*cf.* also Fig. 23D, E).

The evolution of the auditory ossicles (Fig. 111) has been referred to earlier in this book but may be summarized here as follows. The most ancient member of the ossicular chain is the stapes, or stirrup, which has probably been derived from one of the two upper segments of the second or

hyoid gill arch of fishes. In the oldest known amphibians, as in the frog (Fig. 106) the stapes

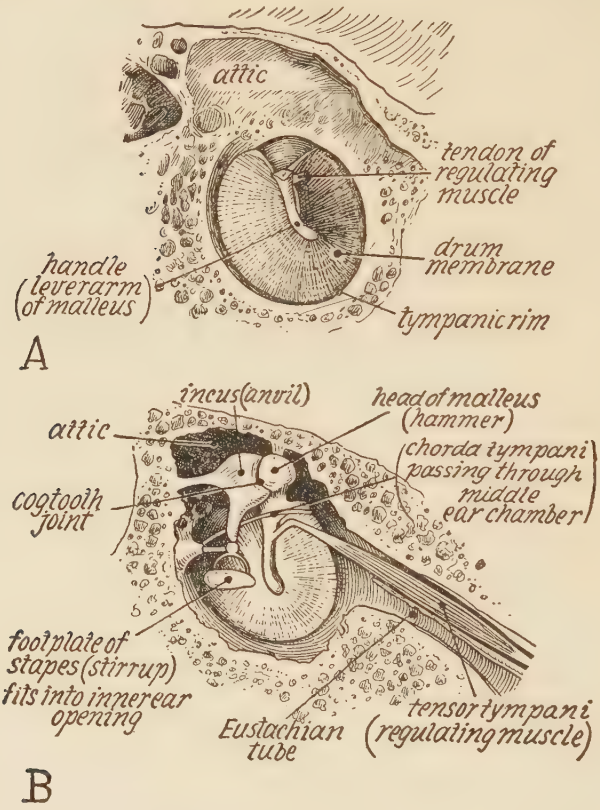

Fig. 111. The Middle Ear of Man, Showing the Auditory Ossicles (after Cunningham).

For details, see p. xxxix.

extends from the inner ear to the tympanum or drum membrane. When the tympanum first appeared (in the Amphibia) it was fastened (Fig.

17B) to the back part of the squamosal bone, or bony shell over the back part of the primary upper

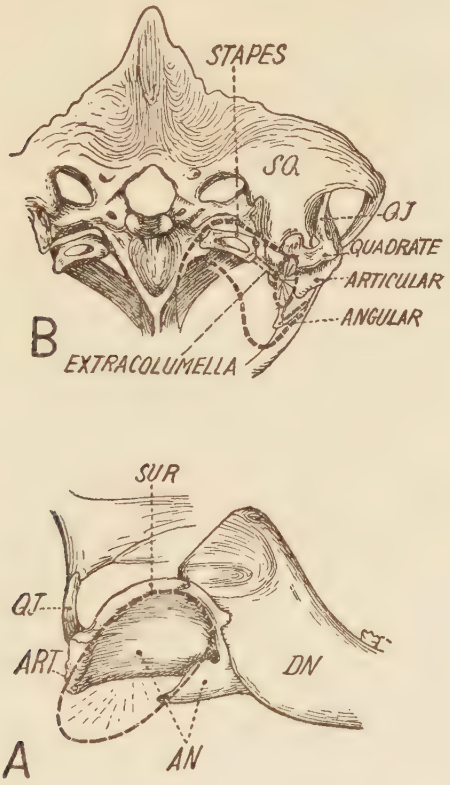

Fig. 112. Relations of the Parts of the Middle Ear in an Extinct Mammal-like Reptile (after Sushkin).

For details, see pp. xxxix, xl.

jaw. In the reptiles the tympanum is always associated with this same region and is also more or less connected with the angular bone of the

lower jaw. In the fossil mammal-like reptiles a large notch (Figs. 112, 113) in the back of the

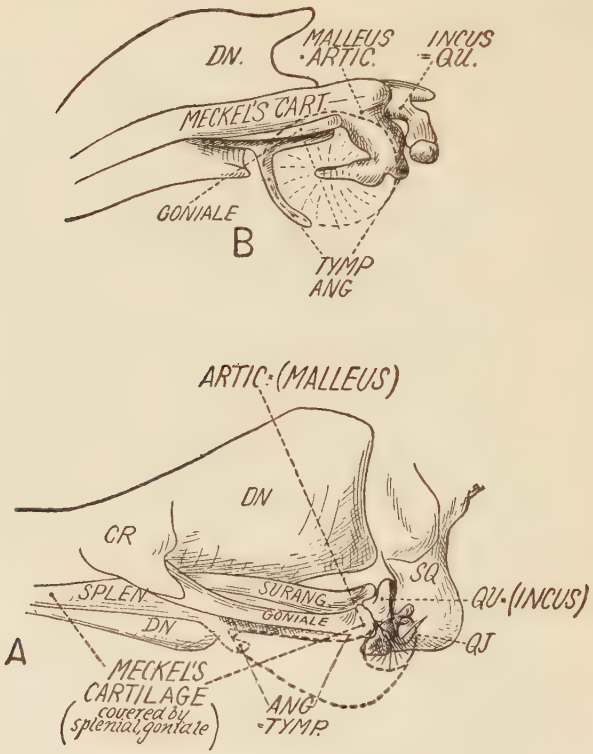

Fig. 113. Origin of Auditory Ossicles.

(A) Back part of the lower jaw of an advanced mammal-like reptile (based chiefly on a cast of the specimen combined with observations and figures of Seeley and Watson); (B) Fœtal mammal (slightly modified from R. W. Palmer). For details, see p. xl.

angular bone is thought for various reasons to have served for the attachment of a pocket from the membranous sac that encloses the cavity of

the middle ear. The stapes was connected with the inner ear on the inner side and by its double outer end (Fig. 112) with both the quadrate bone and the tympanic membrane. When the dentary bone became very large and formed the chief part of the lower jaw, the angular, articular and quadrate elements, which were still connected with the tympanum, became much smaller. When the dentary formed its new joint with the squamosal (pages 36–39) the lower jaw bones that were behind it (quadrate, articular and angular) gave up their function as jaw elements and intensified their auditory function, transforming sound waves into mechanical pulsations and thus transmitting the equivalents of the sound waves to the stapes; this in turn passed them on to the liquid in the inner ear.

In this way arose the marvellous delicate mechanism of the auditory ossicles, the tiny muscles of which (Fig. 111) are still innervated, even in man, by twigs from the main nerve of the jaw muscles. Meanwhile the first gill pouch, below the back part of the jaw, had grown upward and surrounded the now reduced angular, articular and stapes, forming the cavity of the middle ear (Fig. 112).

The human embryo, like that of mammals of all other orders, still shows in the clearest, most undeniable way, the origin of the malleus and incus from the reduced primary jaw elements (Figs. 114, 115).

Ancient and Modern Physiognomy

The art of reading character from the human face is one of the things that every woman knows and every man prides himself upon. But the courts are crowded with the wrongs of deceived women and the prisons are filled with wolves in sheep's clothing who have hidden a ravenous heart behind faces that confident physiognomists, including practical men of business, have diagnosed as honest. What is the matter then with the popular "science" of physiognomy?

To the ancients, never embarrassed by facts, physiognomy was as easy as every other branch of science. Aristotle, according to the Encyclopædia Britannica (article on Physiognomy), taught that noses with thick bulbous ends belong to persons who are swinish; sharp-tipped noses belong to the irascible, those easily provoked, like dogs; large rounded, obtuse noses to the magnanimous, the lion-like; slender hooked noses to the eagle-like,

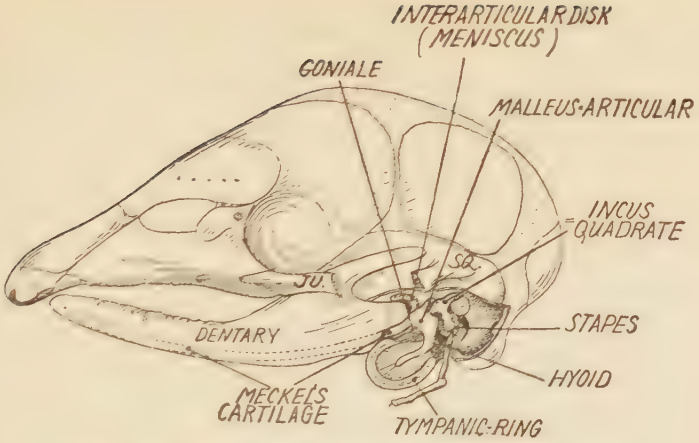

FIG. 114. RELATIONS OF OSSICLES TO LOWER JAW IN FŒTAL ARMADILLO (*Tatusia hybrida*).

(Composed from two figures by W. K. Parker.)

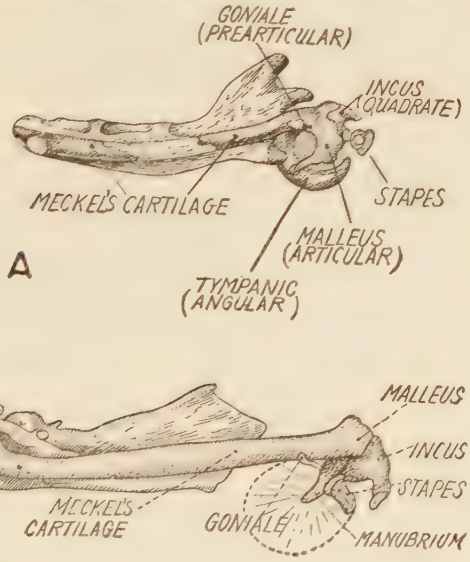

FIG. 115. THE REPTILIAN STAGE IN THE DEVELOPMENT OF THE AUDITORY OSSICLES.

A. Lower jaw and attached auditory ossicles in a fœtal hedgehog (after W. K. Parker). B. Lower jaw and attached auditory ossicles in a human fœtus (after Macklin). For details, see p. xl.

the noble but grasping; round-tipped retroussé noses to the luxurious, like barnyard fowl. This is the kind of rubbish that passed under the name of science for more than two thousand years. Other self-appointed and equally successful teachers classified men and faces as mercurial, saturnine, jovial and so forth, according to the positions of the stars that ruled their fates from birth, so that physiognomy, like palmistry, was clearly linked with astrology.

The modern science of physiognomy, if it be a science, began when artists and sculptors tried to record the facial expressions of emotions and of moral character and when actors tried to reproduce these expressions on the stage. Much valuable descriptive material was thus accumulated and expressions intended to represent piety, devotion, suffering, anger, malice, joy and the like, may be seen in any collection of old masters or any antique treatise on physiognomy.

A great step in advance was taken in 1806 when Sir Charles Bell in his *Essay on the Anatomy of Expression* inferred the action of the mimetic or facial muscles in producing the characteristic expressions of the emotions.

Fig. 116. Young Chimpanzee
Showing Facial Expression.
(From a photograph by Herbert Lang.)

The experimental method of studying physiognomy was founded by Duchenne (*Mechanisme de la physiognomie humaine*, Paris, 1862), who showed that by the use of electricity the action of the separate muscles could be studied and by the aid of photography accurately represented (*Encycl. Brit.*, XI Ed., Art. Physiognomy).

In Darwin's book on the *Expression of the Emotions* (1872) it was shown that man and the apes agreed in expressing equivalent emotions by means of homologous facial muscles (Figs. 23, 24, 116). Thus the subject of physiognomy was brought under the evolutionary point of view.

At the present time the general subject of physiognomy or the systematic investigation of the human face is being pursued according to the following methods. First, the evolutionary method, as in the present work, endeavors to answer the question, by what stages did the human face arrive at its present form? From the evolutionary viewpoint each type of face among the lower animals is associated with a definite pattern of behavior. Hardly a beginning has been made in tracing the evolution of behavior or in correlating the details of facial character with neuro-anatomy.

Second, the anthropological method studies the variations of the face in different races and endeavors to arrive at general concepts of pure and hybrid racial types. Third, the ontogenetic or embryological method describes the development and growth of the head as a whole and of its several parts. Fourth, the genetic method studies the heredity of facial characteristics, tracing through successive generations the results of homozygous and heterozygous matings with reference to particular features. Fifth, the physiological method studies the chemical factors of the growth and development of the face, including those growth-stimulating substances that the embryo derives from its parents and those that are produced by its own various endocrine glands. Sixth, the clinical method notes that certain types of face are frequently associated with low resistance to certain diseases and seeks to determine the causes of this association. Seventh, the psychologic or behavioristic method endeavors to determine whether there are measurable correlations between definite combinations of features and grades of intelligence. Can an expert predict from examining faces alone which individuals will score high

and which low? Eighth, the student of crime and criminals endeavors to discover correlations between certain types of face and constitutional predisposition to crime. Ninth, the psychoanalyst will undoubtedly seek for traces in every face of the sore conflict between the "censor" and the rebellious subconsciousness. Tenth, the psychiatrist, studying pathologic types of mentality, may approach his material from any of the above described paths. Let us see now how much room there is for the old-fashioned physiognomy.

I undoubtedly inherit the general ground-plan of my face from my excessively remote shark-like ancestors who possessed paired olfactory capsules, paired eyes and paired internal ears, arranged in the order named, and who had a medium mouth below the nose and eyes. I also owe to these humble creatures the framework of my tongue and vocal organs, my jaw and throat muscles and many other features both useful and necessary.

Next, I owe to the primitive lobe-finned fishes or crossopts the complete bony scaffolding of the face and jaws, which in them lay on the surface but in my own face is deeply buried beneath the flesh.

Then I owe to the higher mammal-like reptiles

the fact that the right and left halves of my lower jaw are composed of a single piece and that I have a set of teeth limited to the margins of the jaws and differentiated into incisors, canines, premolars and molars. I also owe to these hitherto much neglected animals the "basic patents" for the delicate apparatus of my middle ear, together with my bony palate and several other important parts of my make-up.

In the earliest mammals the bony mask became covered with mobile, sensitive flesh; to them I owe also the very hairs of my head, my eyebrows, eyelashes and other facial accessories.

To my earliest primate ancestors I owe the large size of my eyes and a considerable part of my brains.

To my friendly anthropoid ancestors I am heavily indebted: for eyes that can focus on things near at hand, that give stereoscopic pictures and that follow closely the flight of a moving object; for a nose that is a real nose and not a snout; for lips that can smile and laugh or curl up in anger or kiss in love; from them I inherited all my baby teeth and my thirty-two adult teeth; the very shape of my ears is theirs.

To my early human ancestors I owe the reduction of my hitherto coarse muzzle and the first training of my tongue to speak.

To my later human ancestors I owe the improvement of my forehead, the general refinement of my features and my rather weak jaw.

To the Nordic strain in my ancestry I ascribe my fair skin and blue eyes, while to both the Nordic and the Mediterranean strains I owe my narrow head and a nose of moderate dimensions, conforming neither to the figure-6 type nor to the alpine V, nor to any of the concave varieties, but fairly straight and presentable.

However, when I have determined all this and much more of the same kind I am still far from giving a description of my face that would satisfy the requirements of Scotland Yard, for most of the features mentioned have been true of millions of men of all ages. There remains then not only the exact measurements and proportions but also the individual history of my face.

Fortunately my development proceeded without undue mental stress or sudden prenatal shock. Hence I escaped being a Mongolian idiot. My ancestors do not seem to have had deficient thy-

roids and there must have been a fair sufficiency of iodine in my food, for I missed being a cretin. After birth I never developed any notable deficiency in either the hypophysis, the thyroids, the thymus or other glands, so on all these counts I missed obesity, and on account of the fair state of the pituitary I escaped gigantism and acromegaly; as the adrenals functioned properly, excessive pigment was not deposited in the skin and so I escaped Addison's disease by a wide margin.

Thus owing to all the favorable circumstances of my prenatal development I did not "come into the world scarce half made up" but all the various parts of my face joined together in the right order, with no undue accelerations or delays, and so I escaped many distressing inconveniences such as a hare lip or a cleft palate. At the right time before birth I lost the "Mongolian fold" in the inner corner of my eye; nor was my face marked with a nævus. But after birth I had to run the gamut of children's diseases and no doubt they checked growth to some extent, leaving me with a temporarily impaired heart and a little below the average in stature and weight. On the deficit side also there was a defective turbinate bone

and a slightly warped septal cartilage of the nose, together with slight malocclusion of certain teeth and a failure of two wisdom teeth to erupt.

Thus I may explain my face although I cannot improve it. A specialist in this subject could afflict the reader with many pages of this sort of thing; but the chief object here is to raise this point. Suppose I asked my grocer to open a credit account on short acquaintance; upon which, if any, of the features listed above would he decide to trust me? Would he not trust equally well many other customers with entirely different types of face? And do we not see similar artistic talent, musical talent and traits of leadership, moral courage, etc., embodied in widely different types of face? In short, does not scientific physiognomy and even intuitive physiognomy discount all these and many other such before coming to the small residue of features that may conceivably be correlated with particular mental and temperamental qualities? And in order to detect the abnormal must one not know at sight the normal range of variations in all the features in all the races for both sexes from infancy to old age?

The studies of Keith, Stockard and others on

abnormal human types and of Stockard on the parallelism between abnormal human and animal types are all leading to a new understanding of the causes of racial and individual types of faces. The bulldog and a certain type of human dwarf with a broad face and retroussé nose equally owe their peculiar features to a derangement of the normal functioning of the hypophysis, one of the growth-regulating glands. This condition is called achondroplasia and is largely hereditary. In both the bulldog and the achondroplastic dwarf the base of the skull ceases to grow and becomes ossified at an early stage. The rest of the growing head, being confined at the base, grows out at the side and the head thus becomes short in proportion to its width, or brachycephalic. Similarly the median cartilaginous septum of the nose is not pushed forward by the base of the skull, the bridge of the nose therefore fails to rise up and the nose remains flat or actually sunken, giving a marked depression below the forehead. The maxilla, or upper jaw bone, like the base of the skull, fails to grow forward and this causes the lower jaw to protrude beyond the upper, giving a characteristic "undershot jaw."

The opposite condition to achondroplasia is known as acromegaly and is due to an opposite disturbance of the normal functioning of the hypophysis-pituitary complex. It is characterized by excessive growth of bone in the linear direction. Human acromegalics are apt to become excessively tall, their faces growing exceedingly long and their chins very protruding. Acromegaly is often but not always associated with gigantism, which presumably results from an abnormally active thyroid gland. Among the dogs, writes Stockard, the St. Bernard, the mastiff and some others show symptoms of acromegaly along with gigantism. The bloodhound, on the other hand, is a splendid example of the acromegalic type without gigantism and his facial expression and general appearance are closely similar to the human acromegalic.

The opposite condition to gigantism, known as ateleosis, is responsible for the production of true midgets, which typically grow normally for five or six years after birth and then stop growing. They may or may not become sexually mature and often retain infantile faces. Among dogs the King Charles spaniel is in "shape, outline and expression almost a picture of the human midget" (Stockard).

Quite recently Stockard has classified all human faces under two general types, into which almost all ordinary persons fall, the "linear" and the

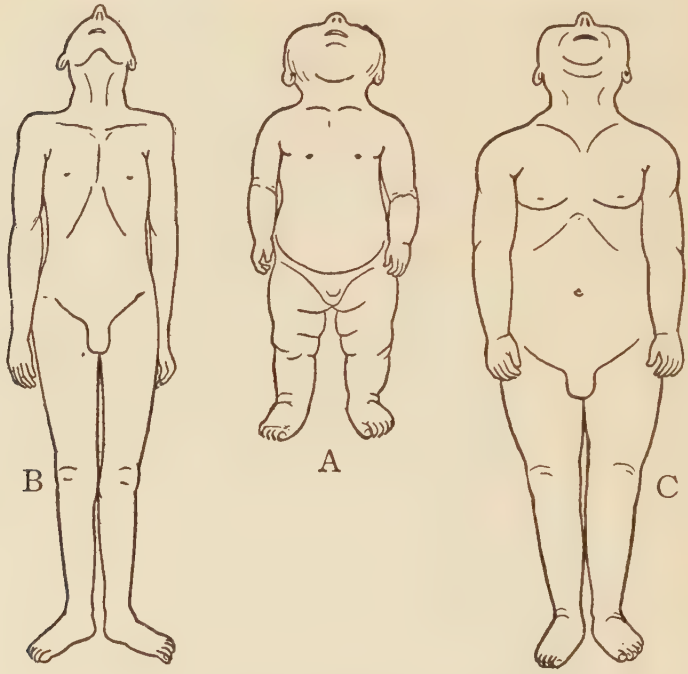

Fig. 117. Stockard's Linear and Lateral Growth Types (after Stockard).

A. Infant; B. "Linear" adult; C. "Lateral" adult.

"lateral" (Fig. 117). His linear type is that in which, owing to a high rate of metabolism induced by a highly active thyroid gland, growth along the long axis of the body (from the tip of the nose down the back) greatly predominates over growth

in the transverse plane. The linear type is the faster-growing, thin but not necessarily tall group. His lateral type, owing to the slower metabolism of low thyroid activity, is slower in maturing and is stocky and rounder in form; that is, the transverse growth components are relatively greater than in the linear type. Stockard's recognition of these two types was a result of his long experimental work on the factors of growth during the embryonic development of animals. His descriptions of the types are of such fundamental importance for an understanding of racial and individual differences in faces that it is necessary to quote them quite fully:

> Taking the tip of the nose as the extreme anterior point of the body and viewing the figure laterally, as seen in figure 1 [118] we may draw a line which would indicate the morphological lateral line. This line on each side of the body separates the truly dorsal from the truly ventral surface regions. When these lines on the two lateral surfaces of the head and body are thought of in space we may imagine that the nearer they come together the more linear is the individual, and the wider apart they diverge the less linear and more lateral the individual type will be. Figure 2 [117] illustrates this in the growth and development of the two types from the infant condition.
>
> Examining figure 2B [117B] it is seen that when the lateral lines are near together the head is of course narrow or dolichocephalic. The interpupillary distance is short and the eyes are close together, the nose bridge is narrow

and therefore generally high, the mouth arch is narrow and for the same reason generally high, the lower jaw is small and narrow and usually not strongly developed.

Fig. 118. Side View of Human Figure, to Indicate the Anterior Tip and the General Direction of the Lateral Line (after Stockard).

The teeth are usually crowded and somewhat ill-set. The neck is long and small in circumference, the shoulders are square, high and angular, the extremities are long and slender with long slender muscles and slender bones, the trunk is short and narrow, tapering to the waist. The intercostal angle is quite acute. The stomach in such a person is long and narrow and rather vertical in position,

extending to low in the abdomen and the liver is generally small.

The shape of the eye in this type is such that it is usually physiologically far-sighted though not pathologically so. They need no glasses on the street unless for astigmatism or some pathological condition. They are under weight for height according to the crude average tables now in use, and are often so as children. They arrive at puberty rather early than late and differentiate rapidly so that the males develop a large strong larynx and a low-pitched bass or baritone voice. Their skin is thin and sensitive as is also the epithelial lining of their alimentary tracts. When in normal health they rarely laugh aloud and when suddenly shocked they resist the reflex jump and never scream. In this way they pass for cool, calm individuals with steady nerve, but as a matter of fact the body is almost constantly held under nerve control and they are actually nervous, usually suffering more after a shock than on the occasion.

The lateral type when fully expressed is the antithesis of the linear type in all of the respects mentioned. The lateral lines are far apart and the head grows wide and not long (Brachycephalic), the interpupillary distance is wide and the eyes are far apart, the nose bridge is wide and often, though not necessarily, low. The mouth arch is wide and low, the teeth are not crowded and are usually smoothly set. The lower jaw is large and strongly developed. The neck is short and large in circumference. The shoulders are round and sloping. The extremities are not long and are stocky with large bones and thick short muscles. The trunk is inclined to be long and full, not constricted but bulging at the waist. The intercostal angle is quite obtuse. The stomach in such a person is large and tends to be transverse and high in position, the liver is generally large.

The eye in the lateral type is so shaped as to be anatomically near-sighted instead of far and such persons frequently wear glasses on the street. This type is well rounded and over weight for height and also shows great fluctuations in

weight, often gaining or losing as much as 15 or 20 pounds in a short space of time. Those of the linear type on the contrary do not experience rapid weight changes but maintain a very constant weight, and may during the twenty years from about nineteen to thirty-nine vary a small number of pounds. The lateral type arrives at puberty a little late and is slow differentiating, the larynx of the male does not develop so suddenly as in the linear type and does not usually grow so large. The voice is thus high or tenor instead of bass. When men are under thirty years old the heaviest bass voices are almost always found among the thin linear individuals and these are very rarely tenors. The finest tenor voices are those of the round lateral type. Everyone recalls that the fine tenor is a fat man while the heaviest bass is a tall thin man.

The two types are more clearly expressed in men than in women since the growth and glandular reactions are more decided in the male than in the female and are also freer from physiological disturbances. Many more physical points of difference and contrast could be cited for the groups but the above list is sufficient to make the differences clear.

The balance between these two opposite growth tendencies is very delicate and during individual development environmental stimuli may deflect the results now in one direction and later in the other, the exact median between the extremes being seldom realized.

As to the inheritance of individual features, Von Luschan, Hooton and other anthropologists have shown that in respect to adult head length and head breadth, nose length and nose breadth and

many similar measurements, the individual tends to resemble either one parent or the other and not an average between the two.

The results of crossing the linear and the lateral types with their opposites are described by Stockard (1921–22, p. 62) as follows:

> Again there are persons who do not properly fall into either type, nor are they typical intermediates, or blends of the two types. These individuals may possess well marked fully expressed features of the linear type along with typically developed lateral features. They may be dolichocephalic with near-sighted eyes, wide palate arches, and tenor voices. Combinations that are at once out of harmony. Such individuals are almost invariably found to be derived from parents of opposite types, and they are very common among the offspring of race mixtures.

Environmental influences may tend either to emphasize or neutralize hereditary tendencies. According to Stockard, Keith and others, a person may inherit from his parents a highly active thyroid gland which under favorable conditions would cause a high rate of metabolism and produce features of the linear type. But owing to disease or deficiency in iodine this person's thyroid may be checked in its activity and he may to that extent acquire lateral features. On the other hand, another person may tend to inherit a more sluggish

thyroid gland, which would give him lateral features, but owing to some environmental stimulus, such as treatment with thyroxin, his thyroid gland may be stimulated to greater activity and to that extent his features may approach the linear type.

Another complication arises from the circumstance that the growing parts themselves show different degrees of response or receptivity to the hormones or growth-stimulating substances secreted by the ductless glands. In the dachshund, for example, the bent legs resemble those of the achondroplastic bulldog, while the long muzzle is like those of ordinary large hounds (Stockard, 1923, pp. 269, 273). Whatever influence produced the achondroplastic limbs would have produced a bulldog-like head, if the growing head itself had been receptive to it.

One goal of scientific physiognomy would be the ability to control and regulate the environmental factors of growth to such an extent that hereditary defects in the facial make-up could be overcome; while a eugenic ideal would be to encourage the increase of strains tending to produce beautiful faces linked with high intelligence and moral worth.

In conclusion, the labors of Keith, Stockard, Davenport, Bolk and of the endocrinologists are slowly bringing modern physiognomy toward the goal of ancient physiognomy, in so far as they tend to the discovery of correlations between particular facial characteristics and psychologic reactions. Thus Stockard, for example, writes as follows, giving his impressions of various physical and mental traits associated with the linear and the lateral growth types:

The basic psychology of an individual is probably associated with his structural type. Two persons of the same race and region that chance to be of opposite types show contrasted mental reactions. The lateral type is careful and painstaking, observing details and valuing them and making little effort to get at the meaning of things or draw conclusions until a mass of detail has been accumulated. This type is emotional and expressive, laughs aloud and shows impulses and feeling towards things, the eyes easily fill with tears and the point of view is rarely concealed. The linear type on the other hand has great difficulty in accumulating detail or in working a subject out thoroughly. These individuals have mild respect for details and tend to draw conclusions and see the meaning of things after only a hurried survey. They are not emotional and do not laugh aloud since their reactions are generally under control and their reflexes are suppressed. They conceal their impulses and would be ashamed to shed a tear. This type is self-conscious and nervous, while the lateral type is not self-conscious and not really nervous in the common sense of the word. The linear type has great self-control and among savage tribes the chief is almost always of this

type, but among civilized peoples the lateral type with near sight and emotion are often rulers of great ability. The lateral type rulers are popular and aware of the details of the immediate situation but are not apt to perceive the great principles of the future. So the linear type Presidents of the United States are honored long after their terms of service, but are often not popular during office, on the other hand, lateral type Presidents perchance of equal ability and equal greatness have been the idols of their time but leave nothing to be remembered in the future.

The Face of The Future

In the United States the Indians as a whole have not readily adopted the ways of the white man and with few exceptions have not been absorbed into the general population. Hence by outside political and economic pressure they have been forced into relatively small reservations where a great increase in their numbers seems improbable. Except in very limited regions Indians have seldom been able to compete for a livelihood with a more or less antagonistic white population. It is hardly likely therefore that a thousand years from now the Indian features will be very common in the population of the United States as a whole. The negro population, on the other hand, is much larger. But the negro is peculiarly liable to certain fatal diseases and particularly in rural

districts infant mortality has hitherto been high. In the cities where mixed bloods occur in large number the constant accession of darker features from the country may more than offset the relatively slow infiltration of white blood. Moreover the white population is so enormously greater than the negro and has such great economic and social advantages and there is such a widespread and deep antipathy to the marriage of full-blooded whites and "negroes" of any shade that it seems highly improbable that the white population will soon absorb the black population *en masse*. Hence it seems unlikely that the *average* white man's face a thousand years from now will show much trace of negroid admixture in the United States as a whole. In many parts of Africa, on the contrary, the whites are so far out-numbered and the climatic conditions are so unfavorable that it seems probable that a thousand years from now the negro, with perhaps some infiltration of white blood, will still be in the vast majority. Thus we see at once that the average face of the future in any given locality will naturally depend first of all upon the relative increase of one or another racial type in the general population.

As to the changes in the face of the white race, Sir Arthur Keith has adduced evidence tending to show that a thousand years ago the average Englishman had a wider face, a shorter nose, a broader palatal arch and better teeth than the typical Englishman of today, who tends toward a narrow face and a narrow-vaulted dental arch. Keith ascribes this in part to the coarser diet and outdoor life of a thousand years ago, which gave the ductless glands that control growth more chance to produce better teeth and better dental arches. Nevertheless there is reason to believe that in spite of the many unfavorable influences today, especially in the cities, living conditions are on the whole more sanitary, as shown by the decreasing mortality. But while there are better conditions for producing healthy children, more of the weaklings are also kept alive to perpetuate their troubles. In any event, it is not unlikely that in the long run eugenic counsels will prevail in the more enlightened countries of the world, at least to a noticeable extent.

Possibly the people of those days may extract all their teeth before they begin to give trouble, or they may be fed with endocrine and other

extracts to combat the ills that we now suffer. In any case it seems not improbable that at least for a long time conscious effort will be directed toward correcting unbalanced departures from the types of face that for thousands of years past have been considered good-looking. From all this it appears probable that a thousand years from now the average adult white person's face will not be profoundly different from what it is today.

But what of the human face a million years from now?—a short period compared with its entire history. If present tendencies continue unchecked the white people of those days will for the most part have lost all four of their wisdom teeth so that their total number of teeth will be twenty-eight. This will tend to make their jaws somewhat slender. If they no longer eat meat and vegetables but take prepared extracts as food, their jaw muscles and jaws may be further weakened. Their brain capacity on the average may be considerably larger. Even under the operation of restrictive eugenic principles there may be at least as great a diversity in normal white faces then as there is today. While some of those people

might look strange to us, others would remind us at least of certain types we had seen in our own times.

In short, the only conservative prediction to make is that the people a million years from now may be far less unlike ourselves than we had at first imagined. But as the determination of the dominant type of human face in the remote future will depend partly upon unpredictable economic and political movements and upon the success in spreading and enforcing eugenic principles, prophecy of any kind is obviously rash.

If, as many geologists suspect, we are now living in an interglacial period and the continental ice-sheet again covers the northern parts of Europe and North America, then a large part of the white population may be driven to the southern United States and Mexico, with consequent tendency to absorb the more or less colored strains of those regions; but on the other hand, many of the white race may persist along the southern borders of the glaciers. Such speculation is only excusable in order to make the point that prediction of the distant future is far less reliable than deciphering the remote past.

Looking Backward

The mobile mask in front of men's brains began to attract our attention when we were babies and continues to fascinate us as long as we live.

Its signals have vital meanings to us: we variously respect, admire, love, hate or are bored by it.

But we cannot escape it. It dominates literature and with its mystical symbolism it broods over religion.

Let Science interrogate the sphinx, let her expose the intricate and delicate mechanism by which the mask is operated, let her even show that the human face, with all its charms, is but the end of a long series of useful improvements upon simple beginnings.

Yet the transformation of the face from fish to man will lose none of its wonder.

Our hearts will still move to the flashing glances of youth; nor will we cherish less the serene, beloved countenance of old age.

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